(US ISSN 0027-4100)

Bulletin OF THE
Museum of
Comparative
Zoology

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CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 151, NUMBER 6
14 SEPTEMBER 1987

(US ISSN 0027-4100)

PUBLICATIONS ISSUED OR DISTRIBUTED BY THE MUSEUM OF COMPARATIVE ZOOLOGY HARVARD UNIVERSITY

Breviora 1952–
Bulletin 1863–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
Occasional Papers on Mollusks, 1945–

SPECIAL PUBLICATIONS.

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SYSTEMATICS AND LEVELS OF COVARIATION IN *CERION* FROM THE TURKS AND CAICOS ISLANDS

STEPHEN JAY GOULD[1] AND DAVID S. WOODRUFF[2]

ABSTRACT. *Cerion*, the most morphologically diverse of all pulmonate genera, has been vastly oversplit in such a way that existing names form an incoherent pattern of variation within and among islands. We have reduced the 300-odd taxa of northern Bahamian *Cerion* to a half-dozen species with consistent and predictable distributions. This study represents our first attempt to apply our ecogeographic and biometric methods to the different *Cerion* fauna of the southeastern Bahamas.

The dozen available names, inconsistently distributed about the islands of the Turks and Caicos banks, reduce to three valid species: *Cerion regina*, present on all islands as Turks and Caicos representative of the "tapering morphotype," the predominant and characteristic *Cerion* of this entire region; *C. lewisi*, a Cuban migrant restricted to islands of the western Caicos Bank; and *C. blandi*, misattributed to the *C. glans* complex in the past, but actually an immigrant population of the *C.* (*Umbonis*) stock, confined to Salt Cay on the Turks Bank and hybridizing with local *C. regina*.

Biometric patterns based on factor analyses of mean vectors for all samples reveal order without exception at a series of descending levels. Clustering of samples can be interpreted as results of meaningful patterns in covariance among measures defining the axes. At the most inclusive level of all samples on all islands, each of three principal axes captures the distinctive morphological features of a taxon. Therefore, axes reflect taxonomic diversity and the contingent histories of migrations. At the next lower level of variation (among samples within *C. regina* on all islands), island groups are distinguished by patterns of covariation that express developmental rules of growth and allometry within a coherent *Cerion* ground plan, not the accidents of history revealed in the higher-level analysis among taxa. A smooth morphometric cline, connecting all islands of the Caicos Bank, unites the two major taxa of previous interpretation into a continuous array, and forms the basis for our decision to synonymize all samples of the tapering morphotype as *C. regina*. At a third level of variation (*C. regina* within our best-sampled island of South Caicos), we detect coherence based upon geometric constraints of growth for any coiled shell. Finally, specimens within samples follow similar patterns of covariance, indicating that general rules of growth apply to the conceptually different styles of within- and among-sample variation.

I. The Problem and Promise of *Cerion*

Copious variation in genetically-resolvable patterns of shell coloration has secured for several pulmonate genera the status of evolutionary "classics" (Cain and Currey, 1963 on *Cepaea*; Crampton, 1916, 1925, 1932 and Murray and Clarke, 1980 on *Partula*; Gulick, 1905 and later studies on Hawaiian *Achatinella*, for example). Yet, although remarkable variation in morphology also distinguishes several pulmonate genera from most other mollusks, this source of insight has not been well exploited by evolutionary biologists—in part because the classic genera for studies of color are not particularly variable in form.

Cerion, a widespread West Indian land snail favoring coastal, carbonate substrates, may be the most morphologically diverse of all pulmonate genera, with variation in shell height from 5 to 70 mm, and in shape from pencils to golf balls. We understand the formal basis for this geometric diversity (Gould, 1984b; Gould and Woodruff, 1986; Woodruff and Gould, 1980), but little of its genetic and developmental foundation. The potential for such unparalleled diversity arises from two aspects of growth: first, the complex, ba-

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sically tripartite allometry of all *Cerion* ontogenies (a juvenile button or triangle, followed by an adult "barrel" with little increase in width accompanying major growth in height, and a final change in coiling before secretion of the definitive adult lip); second, the ordering of growth patterns into several interacting but mutually dissociable covariance sets of coordinated characters. This complex allometry provides great scope for translating small heterochronic effects into major changes in adult form, while the potential independence of covariance sets enjoins both forced correlations within sets (further translating small inputs into complex outputs) and substantial play for novel combinations (by independent change between sets). *Cerion*, in short, is a premier subject for students of form.

Yet *Cerion*'s promise has been impeded by two related "myths" propagated by its traditional literature (particularly Maynard, 1889; Maynard and Clapp, 1919–26). First, *Cerion*'s extreme lability in form has inspired the construction of a bloated taxonomy of some 600 taxa, about half from the Bahamas where we have concentrated our studies (see Clench, 1957). Nearly all named taxa of *Cerion* hybridize freely, and few genuine biological species exist. The second *Cerion* myth holds that the geographic distribution of these formally designated taxa forms a basically incoherent spread, implicating capricious and distant transport by hurricanes as the primary mode of colonization. Admittedly, the placement of existing names on maps implies chaos of this sort, but the traditional taxonomy is fundamentally erroneous (Gould and Woodruff, 1978, 1986, for example).

We have been studying the systematics and biogeography of Bahamian *Cerion* for more than a decade (see literature cited) and have been able to refute these two myths by systematic revision and synonymization of invalid taxa. In our simplified system of biological taxa mapped and studied in the field, the chaos of traditional names breaks down to be replaced by clear order and stable pattern, temporally and spatially, in the distribution of Bahamian *Cerion* among islands.

We have detected order at two basic levels of variation, and have portrayed this coherence primarily by the study of covariance sets, or groups of characters correlated by the general geometries of snail growth and the particular allometries of *Cerion*. We find, first, sensible order within taxa, based upon clines defined geographically (Gould and Paull, 1977 for *C. striatellum*) or ecologically (Gould and Woodruff, 1986 on dwarfing in *C. gubernatorium*), or upon small-scale but discontinuous differentiation among islands (Gould and Woodruff, 1978 on *C. bendalli* in Abaco and Grand Bahama; Gould, 1984a on *C. uva* in Aruba, Bonaire and Curaçao). Second, we have demonstrated consistency in the distribution and interaction of taxa within regions. We find the same forms (or "morphotypes," for we do not know their genealogies) in the same settings from island to island within regions ("ribby" *Cerion* on bank-edge coasts, and "mottled" *Cerion* on bank-interior coasts and island interiors on all major islands of the northern Bahamas, Gould and Woodruff, 1978, 1986). When anomalous taxa invade regions, they occupy restricted areas superimposed upon the underlying predictability of indigenous forms (for example, incursions of the subgenus *C.* (*Umbonis*) into bounded portions of the "ribby" coastal range on eastern Andros, Cat and Long Islands).

II. A Strategy of Research

We have reached the half-way point in our systematic and evolutionary revision of Bahamian *Cerion*. We have studied all major islands of the northern Bahamas (Little and Great Bahama Bank) and have found on each of the eight primary territories (Grand Bahama, Abaco, Andros, New Providence, Eleuthera, Cat, Exuma, and Long Island) the same basic distribution of bank-edge (usually east coast)

"ribby" and bank-interior (usually west coast) "mottled" *Cerion* described above (see Gould and Woodruff, 1986 for summary). In addition, at least two islands (Cat and Eleuthera) harbor relict populations of the major Sangamon taxon from the ca. 120,000 year b.p. dunes of these islands—smooth, white, thick-lipped *C. agassizi*. Finally, a few local incursions of other taxa, usually of the subgenus *C.* (*Umbonis*), have been recorded. The identification of this consistent pattern has permitted us to reduce the bloated taxonomy of Bahamian *Cerion* by more than half, synonymizing some 300 invalid names to a half-dozen or so biological species.

We now extend this program to the genuinely different *Cerion* faunas of the southeastern Bahamas (Inagua, Mayaguana, Crooked-Acklins, and the geographically linked though politically independent Turks and Caicos). The major difference between the two regions is evident by inspection of museum collections. Whereas the ribby-mottled distinction unlocks the northern Bahamas, the main *Cerion* morphotype of the southern Bahamas is an ovate-triangular, generally smooth and white form known by a plethora of names—*C. columna* and *C. christophei* on Inagua, *C. regium* on Castle Island, *C. piratarum* on Mayaguana, *C. regina* on Grand Turk, *C. caicosense* on South Caicos, for example—but sufficiently similar from place to place to provoke a strong suspicion that their underlying unity might provide a key to the southern region. This study is a first attempt to apply the methods that we used successfully in the northern Bahamas to the different fauna of the southern islands, in particular to variation within the "tapering" morphotype (as we shall call it).

We choose the Turks and Caicos islands for this first attempt for two reasons. First, these banks are, geographically speaking, the eastern outliers of the Bahamian complex. Their *Cerion* faunas are simpler than those of larger, more central islands like Inagua. We have had success in our previous work by beginning with sparser faunas of peripheral areas (Gould and Paull, 1977; Gould, 1969a, 1984a) and working towards greater, central complexity (Gould and Woodruff, 1986). Second, several names have been applied on various islands of the Turks and Caicos to populations that may all belong to the tapering morphotype. If we can resolve the current set of unrelated names into a pattern of coherent variation, then we may hope that the southern Bahamas will also yield to a replacement of taxonomic chaos by biological order. In this case, a revision of the entire Bahamian *Cerion* fauna will be within our grasp.

III. The Current Status of the Turks and Caicos *Cerion* Fauna

The available nomenclature for Turks and Caicos *Cerion* provides an excellent example of the systematic problem (systematic, that is, in both technical and vernacular senses) besetting this genus. The Turks and Caicos, spared visits by the most ardent splitters among *Cerion* aficionados, are relatively "underrepresented" by *Cerion* species. Clench's (1957) catalogue lists nine taxa, and two have been added since (Clench, 1961). The existing descriptions give no hint of any order or pattern in the distribution of these supposed taxa on the various islands.

The first eight names were bestowed by Pilsbry and Vanatta in their short paper of 1895 and their catalogue of 1896. Pilsbry, impressed by Maynard's demonstration that the internal teeth and lamellae of *Cerion* shells had taxonomic value, engaged Vanatta to section shells in the extensive collection of the Academy of Natural Sciences of Philadelphia. He thought, in so doing, that he had "brought to light" many new species. In particular, he distinguished for the first time a "Turk's Island" (1895, p. 208) species of *Cerion* from other taxa of the tapering morphotype. He named this first Turks and Caicos species *C. regina* (1895, p. 208), distinguishing it from *C. columna* of Inagua by its more

triangular profile (*C. columna*, as its name implies, is more parallel-sided); from *C. regium* of Castle Island by its smaller size and less thickened apertural lip (as compared with the thick lip of *C. regium*, described in a disparaging and mildly racist manner by Pilsbry and Vanatta as "a lip of quite Ethiopian characteristics"); and from *C. lentiginosum* and *C. album* of Rum Cay by its smoother shell (for the Rum Cay species are costate on their early whorls). Pilsbry and Vanatta then named five subspecies of *C. regina*, in order (pp. 208–209) as *C. r. percostatum* for ribbed shells; *C. r. comes* (literally, the pretty queen) for shells "heavily streaked and blotched with chestnut brown"; *C. r. Swiftii* for smaller, thinner and more triangular shells; *C. r. eucosmium* for smooth, glossy shells with livid, pinkish-brown streaks; and *C. r. brevispira* for short, compact shells. All these names were applied to shells from "Turk's Island," presumably Grand Turk of modern nomenclature. All names refer to common variants of color, ribbing, and size (with engendered covariances in shape) now recognized as the major and pervasive paths of variation throughout the genus.

Pilsbry and Vanatta then recognized a second species from "Turk's Island" as *Cerion incanoides* (1895, p. 209). They noted that "this species belongs clearly to the group of *C. regina*, *lentiginosum*, etc." (loc. cit.), but established a separate taxon to recognize the thin and smooth shell of this form. We do not understand why they made this distinction because, at least to us, collections of *C. incanoides* differ no more from *C. regina* than do several of the *C. regina* subspecies among themselves.

In their 1896 catalogue, a landmark attempt to systematize the entire genus, Pilsbry and Vanatta listed the Turks and Caicos taxa included under and allied with *Cerion regina*. They then named, as *C. blandi* (1896, listed on p. 324, described on p. 334), a genuinely different *Cerion* from this region. They included this thick and solid, small to medium sized, cylindrical rather than triangularly shaped, and strongly ribbed shell in the group of *Cerion glans*, the typical ribby *Cerion* of the northern Bahamas. In so doing, they made an interesting error. *C. blandi*, confined to small Salt Cay of the Turks group, represents an incursion of the distinctive subgenus *C.* (*Umbonis*) that has hybridized to varying degrees with *C. regina* stocks. *C.* (*Umbonis*) has distinctively wavy ribs and incised spiral lines, but these characters are often muted in hybrid forms. In particular, as in *C. felis* of Cat Island and *C. glans irregulare* of northern Andros (both hybrids between an umbonid and *C. glans*), most specimens lack the incised lines and bear strong ribs only moderately wavy. In this "diluted" state, shells of *C. blandi* do superficially resemble standard ribby *Cerion*. Indeed, Pilsbry and Vanatta glimpsed the true status of *C. blandi* in adding to the end of the description: "but the ribs are conspicuously different, peculiarly rough and unfinished, somewhat like *C. felis*" (1896, p. 334). *C. felis* is a *C.* (*Umbonis*) hybrid from Cat Island.

In 1937, Clench described the first *Cerion* from the Caicos islands, establishing the new species, *C. caicosense*. Clench recognized its allegiance with *C. incanoides* and the *C. regina* group, but felt that smaller size, whiter color, and proportions of the apertural teeth (parietal smaller and columellar longer) warranted a new species. We shall show that the Caicos populations, particularly from South Caicos, are distinct biometrically, but for none of the reasons identified by Clench, since all his differentia show overlap with mean values from Turks island populations.

In 1961, Clench wrote a summary paper on land shells of the Turks and Caicos. He properly lumped all previous names for the *C. regina* group, except his own *C. caicosense*, into *C. regina* itself (1961, p. 250), not primarily for morphological reasons, but because all had been described from Grand Turk, and the necessary criterion of geographic distinction for subspecies had not therefore been met. He

retained *C. caicosense* primarily for its geographic separation.

Clench then added two new taxa. First, he described as *C. utowana abbotti* (1961, p. 251) shells from several islands on both Turks and Caicos banks that differed from *C. regina* primarily in the parallel-sided, rather than tapering form of the adult shell. This decision baffles us for two reasons. First, we do not know why he designated these shells as a subspecies of the East Plana Cay form *C. utowana* since its relationships, to us at least, seem so clearly with the local *C. regina* forms. Our biometric work, based on characters that Clench used to distinguish this taxon, places these populations squarely within the *C. regina* field (see section VI C). Second, we do not understand why he distinguished this taxon at all since several populations within *C. regina* share this morphospace in the common continuum from quite triangular to quite cylindrical shells.

Clench then designated as *C. lewisi* (1961, p. 255) an uncontestably different *Cerion* from several islands in the northwestern Caicos. This very thin, strongly mottled, cylindrical, smooth shell looks nothing like any other Turks and Caicos *Cerion*, yet cannot be distinguished conchologically from the highly distinctive *C. lepidum* from nearby parts of Cuba. We do not doubt, as Clench also concluded, that *C. lewisi* is a Cuban emigrant restricted to a few islands of the Caicos Bank.

The existing taxonomy therefore leaves us confused. *C. blandi* (an umbonid incursion probably phasing itself out by hybridization), and *C. lewisi* (a Cuban emigré) are distinct and locally restricted products of probably recent immigration. The prevalent local form, the tapering morphotype that gives the southern Bahamas its *Cerion* "signature," now carries four species names of uncertain status. Pilsbry and Vanatta's *C. regina* has priority, but *C. incanoides* (though synonymized with *C. regina* by Clench) also refers to Turk Island forms. *C. caicosense* has been applied to Caicos island populations, but the basis of its distinction remains unclear. Finally, *C. utowana abbotti* has been described from both banks, but with no evident differences from the *C. regina* incumbents. Moreover, no one has ever claimed any consistent or simplifying pattern in the geographic distribution of the *C. regina* complex in the Turks and Caicos islands. A resolution of *Cerion* on these banks must evidently center on a proper characterization and mapping of morphological differences within the *C. regina* group.

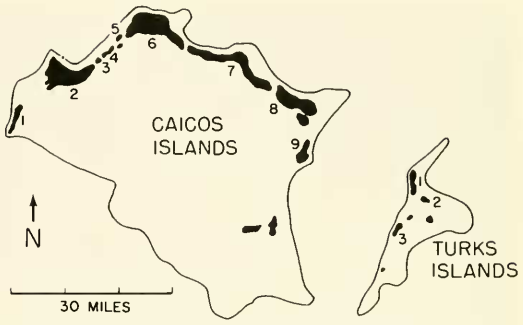

Figure 1. Islands of the Turks and Caicos banks. Turks: 1, Grand Turk. 2, Long Cay. 3, Salt Cay. Caicos: 1, West Caicos. 2, Providenciales. 3, Pine Cay. 4, Water Cay. 5, Parrot Cay. 6, North Caicos. 7, Grand Caicos. 8, East Caicos. 9, South Caicos.

IV. Materials and Methods

We have based our systematic revisions of *Cerion* on biometric and genetic studies of animals collected personally in the field as we map the ecologic and biogeographic distribution of *Cerion*. (We have often, as here, augmented our own material with samples from Museum collections representing populations no longer extant or difficult of access.) In May–June, 1978, we visited the Turks and Caicos to study the geographic and ecological distribution of variation in the tapering morphotype. We collected extensively on South Caicos, sampling every population that we could locate; we then sampled less fully on the largest and most distant island of the Caicos Bank (Providenciales), and on the major island of the Turks Bank (Grand Turk).

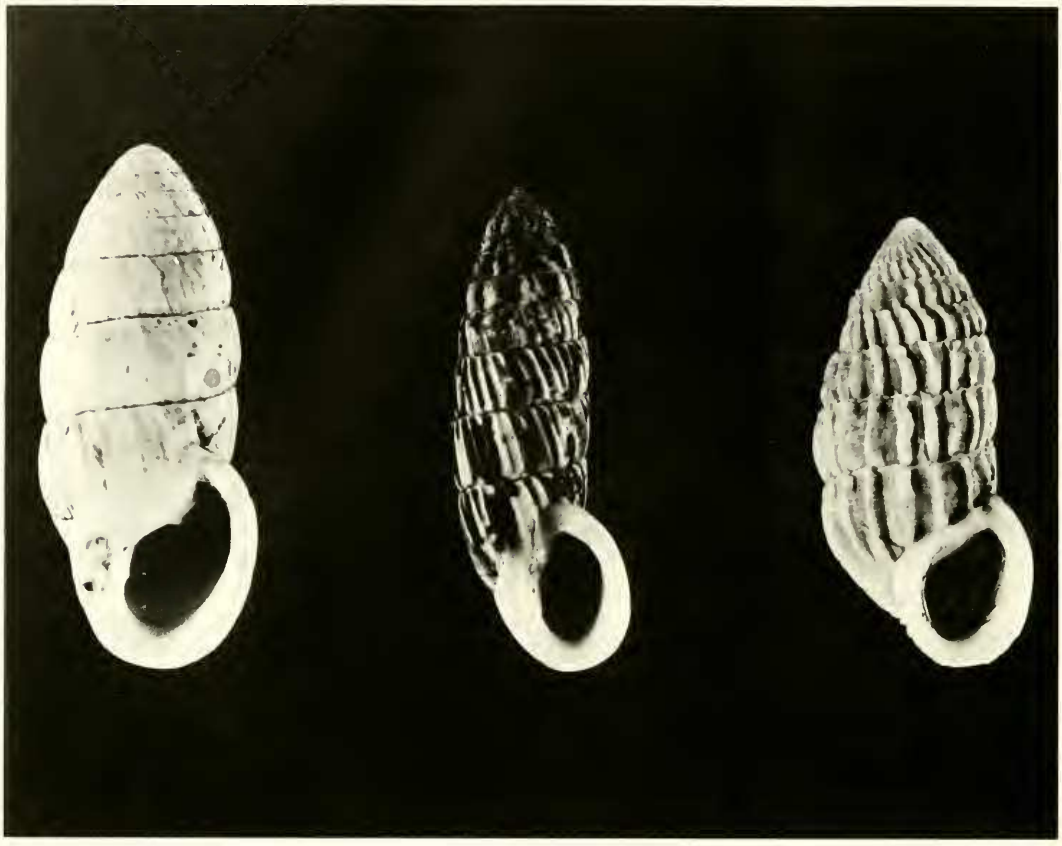

Figure 2. Representative specimens of the three *Cerion* taxa of the Turks and Caicos. Left, *C. regina* from South Caicos, our sample 753. Middle, *C. lewisi* from Parrot Cay, Caicos Bank, MCZ No. 221566. Right, *C. blandi* from Salt Cay, Turks Bank, MCZ No. 220913. Note characteristic *C.* (*Umbonis*) features of *C. blandi*: wavy ribs and incised lines perpendicular to the ribs. The *C. regina* specimen is 34.0 mm high.

We used 29 of our own samples for our morphometric analysis, 23 living and six subfossil. These include 19 from South Caicos (14 living, five subfossil), seven from Grand Turk (six living and one subfossil), and three from Providenciales (all living).

We then selected 32 additional samples for biometric analysis from the collections of the Department of Mollusks at the Museum of Comparative Zoology. These include 15 samples of the tapering morphotype (13 from islands that we had not visited, and two from South Caicos—the paratypes of *C. caicosense*, and *C. utowana abbotti*, both taxa that we regarded as ripe for synonymy). In addition, we measured ten samples of *C. blandi* and its hybrids with tapering forms, all from Salt Cay on the Turks Bank, and seven samples of *C. lewisi* from the western Caicos (West Caicos, Providenciales, Pine Cay, Water Cay, Parrot Cay and Ft. George's Cay). Thus, our set of 62 samples represents all taxa (including types and paratypes, where available), on all islands of their recorded and available distribution. Samples are listed individually in the appendix with their field or museum numbers and their location. Figure 1 shows the islands of both banks, while Figures 2 and 3 display the range of form within the Turks and Caicos *Cerion* fauna (Fig. 2 the contrast among

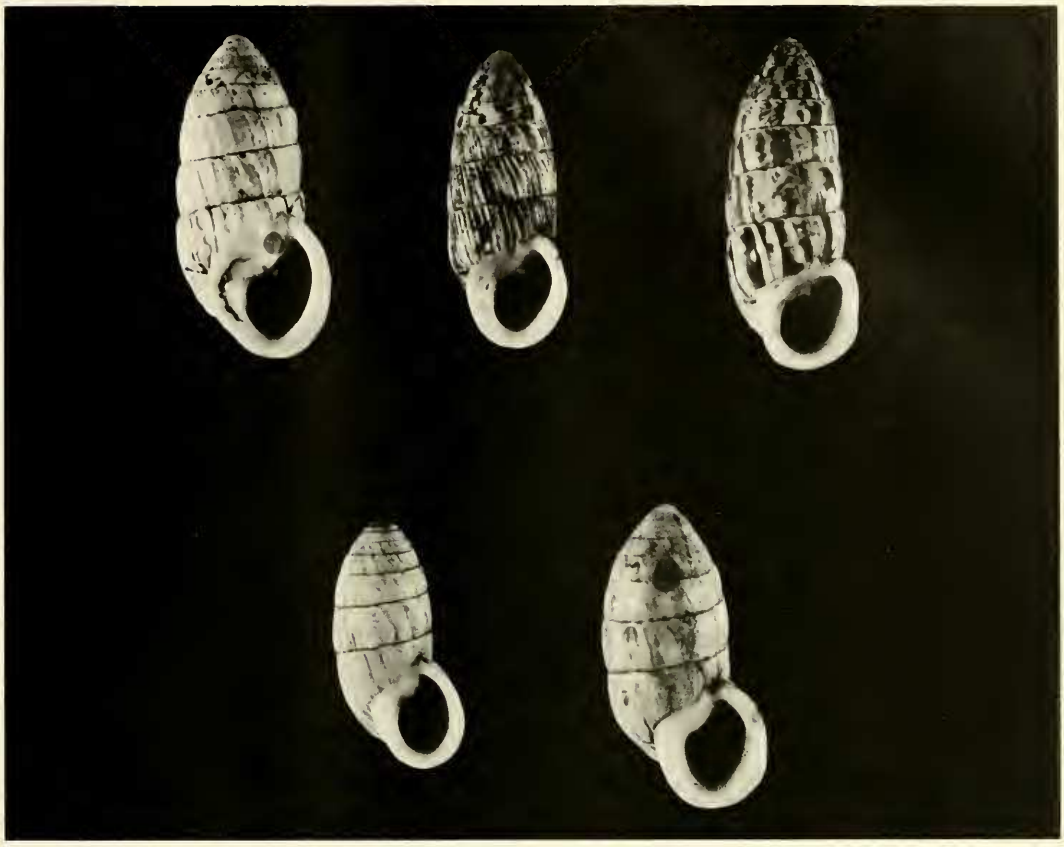

Figure 3. Representative specimens for variation within *C. regina.* Top row, the three islands represented in our personal collections. Left, South Caicos from sample 753. Note the relatively squatter apex—the key defining feature of South Caicos populations. Middle, more apically pointed, finely ribbed and mottled specimen from Providenciales, sample 771. Right, large and apically pointed specimen from Grand Turk, sample 781. Bottom row, representative specimens from paratype samples of two other designated species from South Caicos, both in our view synonyms of *C. regina.* Left, *C. caicosense.* Right, *C. utowana abbotti.* The upper row left specimen is 33.5 mm high.

the three recognized taxa; Fig. 3 the range of variation within the tapering morphotype, here treated as a single species *C. regina*).

For the biometric analysis, we selected 20 adult specimens at random from each sample and measured, for each shell, 18 characters and four additional derived ratios; this study therefore rests upon more than 20,000 direct measurements upon some 1,200 specimens in 61 samples. We have followed the protocol for measurement and analysis used in our recent work (especially Gould and Woodruff, 1986, explained more fully in Gould and Woodruff, 1978), and will not repeat the details here. Table 1 describes and lists the characters, and Figure 4 displays the points for measurements of the aperture and last whorl. The 22 measures used here include 19 of our previous set of 21 (excluding number of ribs on the 4th and 6th whorls because smooth shells of the tapering morphotype lose their juvenile ribs by this stage), plus three basic indices of shell shape (height to width ratios of the protoconch, of the final adult shell, and at the end of the fourth postprotoconch whorl) found

TABLE 1. BRIEF DESCRIPTION OF MEASURES USED IN THIS STUDY (GIVEN IN ORDER OF ARRAY IN SUBSEQUENT TABLES).

1. PROWID	Width of the protoconch
2. FOURWID	Width of shell at the end of the fourth whorl
3. NUMWHO	Total number of whorls, counting from the end of the protoconch as zero
4. RIBDENS	Number of ribs in 50 micrometer units at the end of post protoconch whorl 1
5. LENGTH	Total length of the shell
6. WIDTH	Total width of the shell
7. PROHT	Height of the protoconch
8. FOURHT	Height of shell at the end of the fourth whorl
9. FRSXHT	Height of shell from the end of the fourth to the end of the sixth whorl
10. UMBWID	Maximum width of the umbilicus
11. LIPWID	Maximum width of the lip
12. LIPTHK	Maximum thickness of the lip
13. APHT	Height of the aperture AB′ of Fig. 4
14. APWID	Width of the aperture C′D of Fig. 4
15. APROT	Projecture of apertural lip beyond outline of previous whorls, C″D of Fig. 4
16. EC	Distance from last suture to umbilical border of aperture, measured perpendicular to the suture, EC of Fig. 4
17. FA	Distance from last suture to parietal border of aperture, measured perpendicular to the suture, FA of Fig. 4
18. APTILT	The ratio EC/FA, a measure of the tilt of the aperture
19. WEIGHT	Weight of the shell
20. HWRATIO	The ratio of height to width of the shell, measures 4/5
21. PRORAT	Width/height ratio of the protoconch, measures 1/7
22. FOURRAT	Width/height ratio of the shell at the end of the fourth whorl, measures 2/8

useful in our study of sinistral *Cerion* (Gould, Young and Kasson, 1985). The mean values for all measures in all samples are given in the appendix.

Our measures are chosen to record the major shell characters used to make taxonomic distinctions, including sizes and shapes of protoconch, adult shell, and intermediate whorls; size, form and orientation of the aperture and umbilicus; ribbing and shell thickness; and size and form of the apertural lip. We have also included measures that will permit a reconstruction of basic coiling geometries, following both the analytical schemes of Raup (1966, for example) and the actual, more complex allometries of *Cerion*. *Cerion* is a nearly ideal animal for biometric research. The transition from protoconch to later growth is clearly marked, providing a clear and natural criterion for numbering whorls. Unlike most mollusks, *Cerion* possesses a definitive adult form; as growth reaches its termination, the direction of coiling shifts, the shell overgrows its previous whorls slightly, and then deposits an expanded and thickened adult lip, ceasing all growth thereafter. Thus, we can measure the adult size of *Cerion* shells, without confounding ontogenetic and static variation—a primary source of confusion in most biometric studies of snails.

Two aspects of our research program suggest a factor analytic approach as most appropriate for our analysis: first, because we wish to explore the distribution of samples in the general *Cerion* morphospace (rather than trying to test distinctions, taxonomic or otherwise, previously proposed); second, because our primary interest in the inductive study of morphology centers upon covariance sets, or groups of associated characters often flagged so well by various rotations of factor axes.

Consequently, we have portrayed each sample by its vector of means (see appendix), submitted these vectors to transformations that weight characters equally (percent-range), normalized the vectors to equal length (so that allometric effects will be expressed as shape and simple size difference will not swamp more subtle associations), and then performed our factor analyses on the transformed matrix of mean vectors. (Our analyses are in the less usual, or "inverted," Q-mode format, with loadings as samples and scores as variables, rather than in the more conventional

R-mode—see justification and empirical demonstration of equivalency between the modes in Gould and Woodruff, 1978, 1986.)

The problems presented by variation among *Cerion* samples of the Turks and Caicos may be conceptualized as a descending series of levels, each posing different questions and capturing different information. First, the positioning of all samples in a general morphospace to demonstrate the role of historical contingency in shaping the fauna by bringing two allochthones (the umbonid *C. blandi* and the Cuban import *C. lewisi*) into primary territory of the tapering morphotype. Second, the positioning of tapering samples within the morphospace set by the tapering morphotype itself to see whether any simplification of pattern might replace the current, chaotic taxonomy. Third, the positioning of samples from South Caicos alone within their own morphospace to explore, for our best and most abundantly sampled island, any order in local variation that would probably be swamped by inter-island and inter-taxon effects at the higher two levels. Fourth, and finally, the ordering of specimens within samples (this last being, of course, a break with, rather than a smooth descent from, the previous three levels, since it treats within-sample variation of specimens rather than between-sample variation of mean vectors).

We are interested not only in relationships among objects (as discussed above) but also in the associations of variables that build major dimensions of the morphospace, for the covariance sets thus defined act as constraining channels of variation that both limit the kinds of variation expressed, and also provide opportunity for generating large and diverse changes of form from small inputs (via correlated consequences). The tension between these superficially contradictory but linked themes of limitation and amplification defines *Cerion*'s major interest to students of morphology.

We complemented the biometric study with a survey of genetic variation in snails

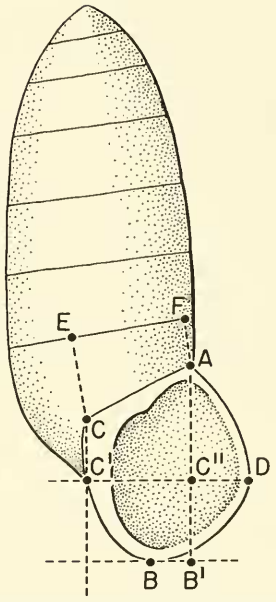

Figure 4. Sketch showing points that define our measures of the aperture. See Table 1.

of the tapering morphotype. Our survey involved more than 520 individual adult snails representing 16 populations distributed among the islands as follows: Providenciales: 2, South Caicos: 13, Grand Turk: 1. One population from South Caicos (site 758) was represented by two subsamples: 758T from a single coconut palm tree and 758 from the surrounding grass and shrubs. In most cases the same individual animals were used for both conchological and genetic study. All samples were taken by searching an area of typically 10 m^2 (a fraction of the neighborhood size) and collecting every adult encountered.

Genetic characterization was based on an examination of individual variation in 16 proteins (Table 2) extracted from foot-muscle tissue. Variation was detected by horizontal starch gel electrophoresis under conditions we have described elsewhere (Gould and Woodruff, 1986; Woodruff, 1975). Using the BIOSYS-1 computer program (Swofford and Selander, 1981) we calculated allele frequencies for each sample together with measures of genetic variation including mean number of alleles per

Table 2. Enzyme systems analyzed in Turks and Caicos *Cerion*.

Protein name (E.C. Number)	Abbreviation	Loci	Conditions*
Aspartate aminotransferase (2.6.1.1)	*Aat*	1	A
Ceruloplasmin	*Crp*	1	A
Esterase α-naphthyl acetate (3.1.1.1)	*Es*	3	B
General protein	*Pr*	1	B
Glucose phosphate isomerase (5.3.1.9)	*Gpi*	1	B
Glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12)	*Gapd*	1	A
Lactate dehydrogenase (1.1.1.27)	*Ldh*	2	A
Malate dehydrogenase (1.1.1.37)	*Mdh*	2	B
Phosphoglucomutase (2.7.5.1)	*Pgm*	2	B
6-Phosphogluconate dehydrogenase (1.1.1.44)	*6pgd*	1	B
Superoxide dismutase (1.15.1.1)	*Sod*	1	A

* Electrophoretic conditions: A = tris borate EDTA buffer, pH 8.6, 250 volts, 4 hrs; B = tris citrate buffer, pH 6.7, 159 v, 4 hrs.

locus ($\bar{A}$), proportion of polymorphic loci (P), and mean individual heterozygosity by direct count ($\bar{H}$). We performed χ^2 goodness-of-fit tests and also calculated exact probabilities to test for random mating. Wright's (1978) F-statistics were used to assess the extent of genetic differentiation within and between samples and also to test for panmixia. Nei's (1978) unbiased measures of genetic identity (I) and genetic distance (D) were calculated for all pairwise comparisons of samples.

V. Covariance at Level One: The General Pattern

In Figure 5, we plot the loadings of all 55 modern samples (excluding only the six fossil samples) on the first three axes (93.7% of all information) of a varimax rotation for a factor analysis of the matrix of mean vectors. (In this triangular plot, the three loadings for each sample are normalized to a sum of 1.0, thus providing a representation of three dimensions in two, with axes at each corner of the triangle. All but one sample have communalities above 0.87, and this procedure introduces very little distortion of relationships among samples. The strongly dwarfed tapering sample from Sand Cay is the sole exception, with a communality of 0.36; nearly all its remaining information lies on a fourth axis defining it alone.)

The evident order of morphological distribution among samples emerges as a pleasing first result; the lack of pattern in existing taxonomies is, as we had predicted and as we have found in all our *Cerion* work elsewhere, an artifact of definition. The three axes are foci for the three major kinds of *Cerion* on the Turks and Caicos—the indigenous tapering morphotype and the two localized immigrants, *C. blandi* and *C. lewisi*. The most distinctive form, pencil-thin and strongly mottled *C. lewisi*, defines the second axis, and all its samples cluster in a small space of high values. The first axis is a referent for tapering samples, and we can already discern clear order in geographic clustering among islands (discussed fully in the next section on the morphospace of tapering samples alone). In particular, all samples from South Caicos occupy a small, unique field nearest the first axis. *C. blandi* occupies a broader field, high on the third axis, overlapping slightly with samples of the tapering morphotype (with which it hybridizes).

The matrix of factor scores (Table 3) defines the bases for distinctions on these axes. When we consider such covariances for a matrix of samples from a single morphotype generated by a single pattern of growth (see next section), then associations of variables tend to record pathways and constraints of development, and factor

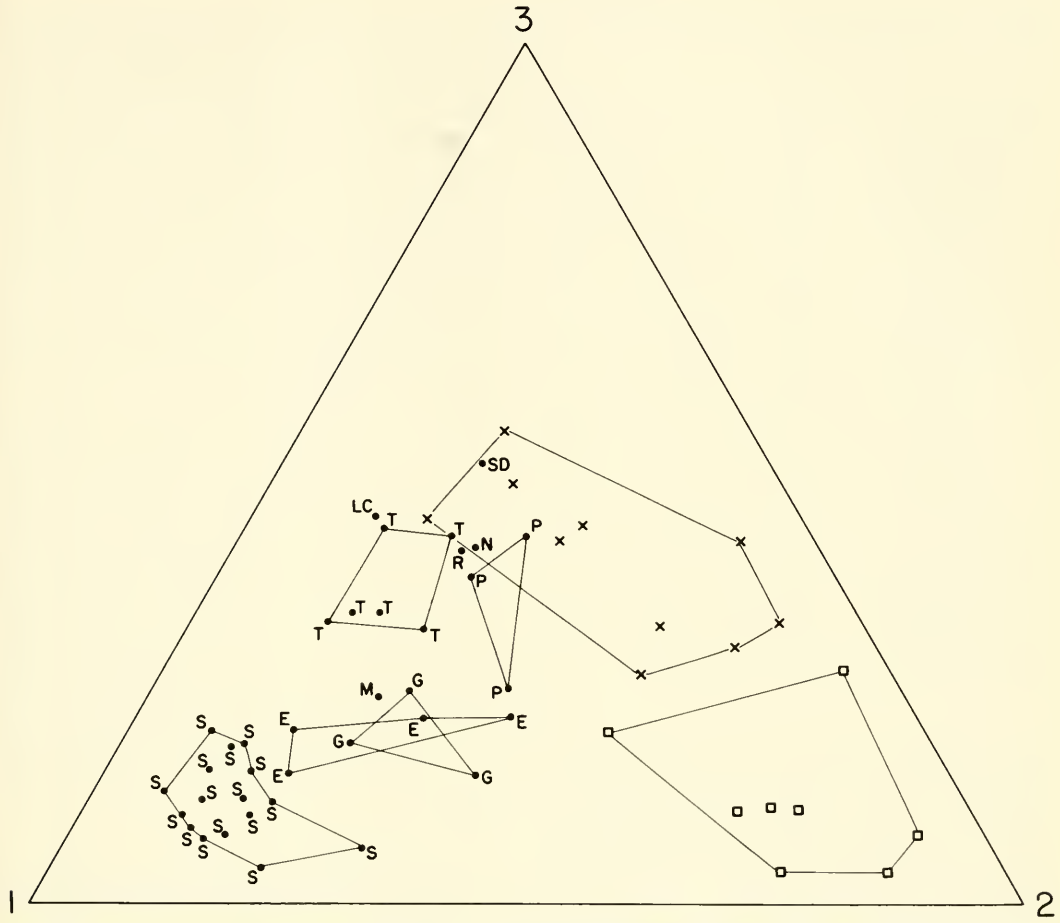

Figure 5. Normalized factor loadings of mean vectors for all nonfossil samples upon the first three varimax axes. Crosses are *C. blandi*, squares *C. lewisi*, and dots *C. regina*. Island for *C. regina* identified as: S, South Caicos; E, East Caicos; M, "Middle" Caicos; N, North Caicos; G, Grand Caicos; P, Providenciales; T, Grand Turk; LC, Long Cay of Turks Bank; SD, Sand Cay of Turks Bank; R, island unknown. Convex polygons are drawn around all samples of *C. lewisi*, *C. blandi*, and *C. regina* from South Caicos, East Caicos, Grand Caicos, Providenciales, and Grand Turk.

analysis becomes a chief tool in the inductive study of constraints and adaptation. But variation lies at too high a level for such an interpretation here because the differences "picked out" by the axes are not dimensions of growth within a coherent form, but the differentia of taxonomic entities forced into the same analysis only by historical contingencies of immigration. Thus, the factor scores of this analysis are records of the basic morphological separation among taxa haphazardly assembled by nature.

The high scores on the second axis all record the chief distinguishing features of its focal cluster, *C. lewisi*—the coordinated characters of a very slender shell achieved by growing many whorls of normal size, not by whorls of unusual height. The shell begins high (0.349 for protoconch height), but height of later whorls do not score strongly. The most distinctive character of slimness (height/width of adult shell at 0.569) is achieved by growing a large number of whorls (0.413), an efficient path to relative narrowness since

TABLE 3. FACTOR SCORES FOR THREE-AXIS SOLUTION (93.7% OF INFORMATION) FOR ALL NONFOSSIL SAMPLES.

Measure	Axis 1	Axis 2	Axis 3
1. PROWID	0.124	0.076	0.141
2. FOURWID	0.269	−0.157	0.265
3. NUMWHO	0.055	0.413	−0.048
4. RIBDENS	−0.093	0.407	0.105
5. LENGTH	0.182	0.233	0.056
6. WIDTH	0.211	−0.079	0.229
7. PROHT	−0.294	0.349	0.493
8. FOURHT	−0.058	−0.030	0.489
9. FRSXHT	0.282	−0.061	0.191
10. UMBWID	0.119	−0.050	0.391
11. LIPWID	0.177	0.046	0.074
12. LIPTHK	0.249	0.020	−0.059
13. APHT	0.230	0.040	0.059
14. APWID	0.253	−0.013	0.037
15. APROT	0.143	0.067	0.129
16. EC	0.236	0.135	−0.022
17. FA	0.171	0.273	0.051
18. APTILT	0.084	0.092	0.032
19. WEIGHT	0.138	−0.027	0.178
20. HWRATIO	0.030	0.569	−0.212
21. PRORAT	0.414	0.086	−0.222
22. FOURRAT	0.353	−0.051	−0.097

the standard allometry of *Cerion* adds height but little or no width throughout middle to late growth (see Gould, 1984b). The numerous fine ribs of this species also distinguish this taxon (0.407) from all other Turks and Caicos *Cerion*.

The third axis, focus for *C. blandi*, records its highest scores for characters well known (see Clench and Aguayo, 1952) as distinct features of its peculiar subgenus *C.* (*Umbonis*)—a wide umbilicus (0.391) and high early heights (0.493 for the protoconch, 0.489 at the end of the fourth whorl). *C.* (*Umbonis*) grows a thin, tapering triangular top by rapid excursion in height, however much the shell may broaden out later in ontogeny.

Scores on the first axis, focus for tapering samples, are more complex because they record two distinct sources of variation—first, a basis of separation between tapering samples and the other two taxa; and, second, the major source of geographic division within tapering samples (note the contrast of South Caicos samples with all others). For the first source, tapering samples are most evidently distinct from other taxa by their generally larger shell size. We find this size difference recorded in the usual manner of factor analytic studies (see Jolicoeur, 1963, 1984)—fairly low and uniform values (averaging about 0.2 in this case) for all measures of basic dimensions in the adult shell (length, width, aperture length and width, sizes of last whorls, that is, measures 5, 6 and 13–17). Standardized sizes of late whorls (fourth width at 0.269, and fourth to sixth height at 0.282) also covary with final sizes.

However, since South Caicos samples load most highly on this axis, we find in addition to these low and uniform scores for general size a few higher scores for distinctive South Caicos characters (see next section), particularly the high values (0.414 and 0.353) for early shell shape (width/height ratios of protoconch and fourth whorl). The relatively flat apices (rapid early growth in width unmatched by height) of South Caicos tapering samples are their chief distinguishing character, both visually and biometrically (see appendix).

VI. Genetics and Morphometrics at Level Two: A Taxonomic Resolution of the Tapering Morphotype

A) The General Pattern: Resolution of Outliers

Figure 6 is a triangular plot of mean vectors for tapering samples alone in their own morphospace. Each island occupies a restricted field arrayed between the first two axes, thus affirming the most important conclusion that we have reached, in study after study, of geographic variation within *Cerion* taxa (Gould, 1984a; Gould and Woodruff, 1978 for example): geographic coherence of shell form marks all *Cerion* distributions; the signature of places is never obliterated.

The array contains an outlier, the strongly dwarfed population from Sand Cay, Turks Bank. Its distinctness is exag-

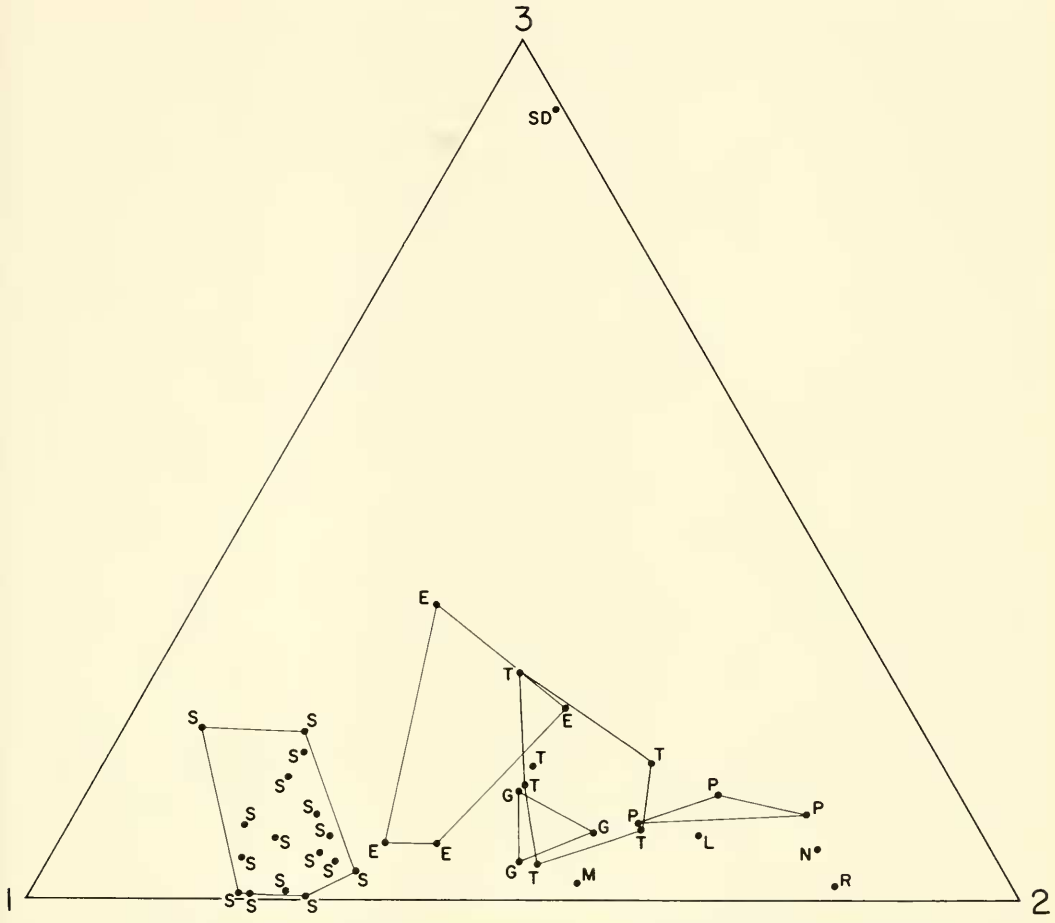

Figure 6. Normalized factor loadings for *C. regina* samples only. Symbols as in Figure 5.

gerated in Figure 6 because factor analysis in varimax rotation tends to absorb uniquenesses on separate axes. The distinctive features of Sand Cay are abstracted by this axis; when plotted into morphospaces that do not include this dimension (as in Fig. 1), Sand Cay plots near all other populations of the tapering morphotype on Turks Bank.

The designation of Sand Cay's uniqueness by an entire axis compresses all other variation into the smaller space of two dimensions. Thus, to expand the portrayal of normal-sized samples in the tapering morphotype, we eliminated the Sand Cay population and repeated the analysis, plotting the triangular diagram as Figure 7. Note that the ordering of normal-sized samples is thereby spread out, but not in any way altered (compare Figs. 6 and 7). The basically linear array of South Caicos-East Caicos-Grand Caicos-Providenciales remains. This array is compressed into two axes on Figure 6, but expanded to three in Figure 7, as the sequence remains fixed in second axis projections, while *each island* now spreads out along the domains of axis one and three.

The Sand Cay population bears, by Clench's own decision (as curator of Mollusks at the Museum of Comparative Zoology), the name *C. utowana abbotti*, one

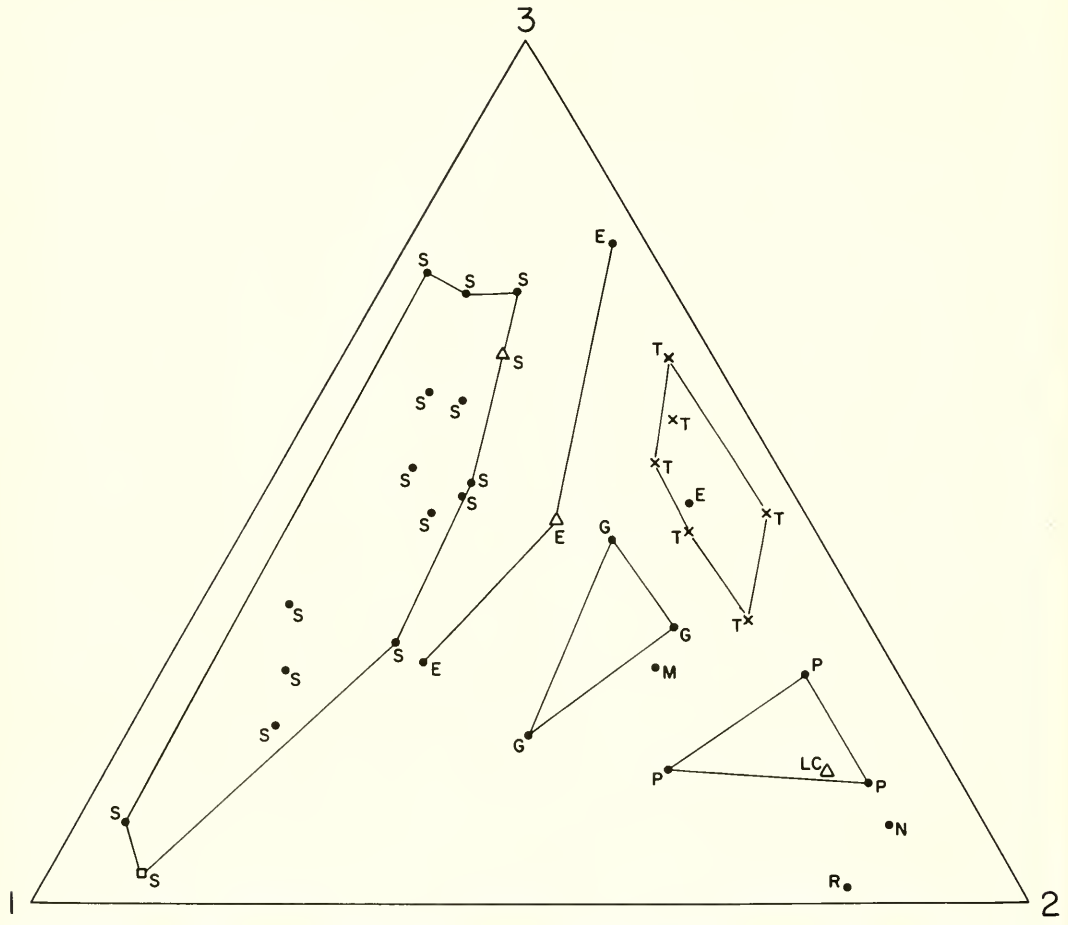

Figure 7. Normalized factor loadings for all *C. regina* samples excluding the Sand Cay dwarfs. Open triangles are samples designated *C. utowana abbotti* by Clench. The open square is the paratype sample of *C. caicosense*.

of the disputed taxa within the tapering morphotype—so one might suspect the validity of this taxon on morphological grounds. But three other samples designated by Clench as *C. utowana abbotti*, including the paratypes from South Caicos, plot (as we shall discuss in part C of this section) at expected positions for their islands within the tapering morphospace. Sand Cay's uniqueness is a consequence of its dwarfing—a simple alteration that provokes, via *Cerion*'s allometries, a large suite of complex changes producing a large overall excursion for the morphological vector considered in toto (see Gould, 1984b; Gould and Woodruff, 1986 for other morphometric analyses of dwarfing in *Cerion*).

The Sand Cay population is not the only strongly dwarfed sample of the tapering morphotype. A subfossil sample from South Caicos (765) yields an even more distant outlier attributable to dwarfing; (see Fig. 8 on the representation of all samples, including the subfossils. Note that axes two and three are reversed relative to Fig. 5, but that the ordering of samples and clusters is not altered). Note that the subfossil

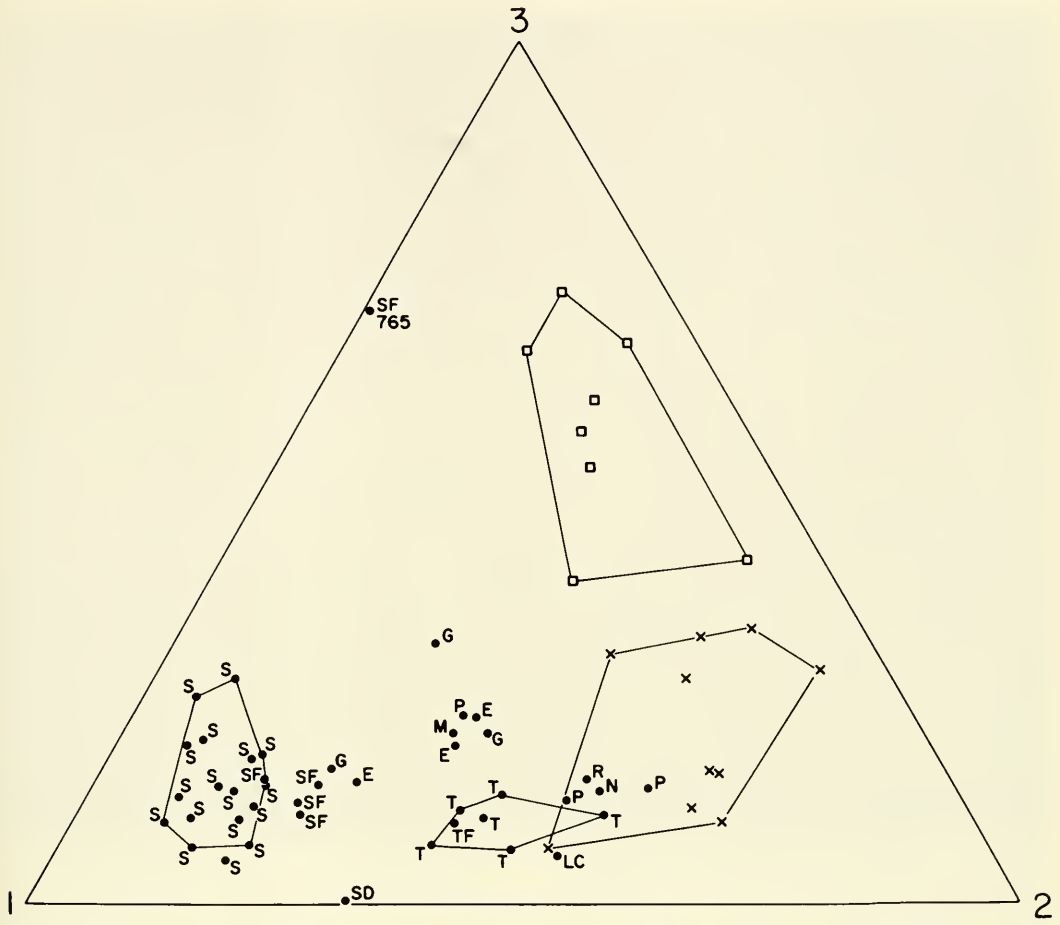

Figure 8. Normalized factor loadings for all samples, now including fossils. Symbols as on Figure 5 with the following additions for fossils. SF, South Caicos fossils (note their position adjacent to but outside the polygon of modern South Caicos samples); TF, Grand Turk fossils; and SF765, smokestack dwarf fossils from South Caicos.

and Sand Cay dwarfs occupy outlying positions at the *opposite* ends of third axis projections.

Fortunately, as the result of a prior study in *Cerion*'s dwarfing (Gould, 1984b), we can identify the common basis in growth and allometry of these apparently contradictory morphological excursions in the two dwarfed populations (see Gould, 1984b). Axis three is the focus in Figure 8 for pencil-thin *Cerion lewisi*. The subfossil dwarfs, projecting as strongly on the third axis as any *C. lewisi* sample, are verging towards "smokestacks" in the terminology of Gould (1984b)—that is, they become dwarfed by restricting whorl size while growing a normal number of whorls. Since *Cerion* increases in height but not in width as later whorls are deposited, this style of dwarfing adds height for a usual amount of coiling to the narrow base of dwarfed whorl size, producing a slender shell. But the Sand Cay dwarfs are "double whammies"—that is, dwarfs through the twin action of reduced whorl size *and* decreased whorl number, leading to squatter than average

Figure 9. Two distinct styles of dwarfing in *C. regina*, producing the major outliers in this species. Left: two specimens from sample 765, South Caicos. Note relative thinning of these smokestack dwarfs with respect to the normal (central) specimen from sample 756, South Caicos. Right: two specimens of Sand Cay dwarfs. Note relatively squatter shells of these "double whammy" dwarfs compared with normal specimen. Leftmost dwarf is 19.1 mm high. Central specimen is 34.9 mm high.

shells through the suppression of whorls that would add height without width. They therefore plot at the opposite end of axis 3, the focus for high-spired *C. lewisi*. This structural understanding of dwarfing and its allometries resolves two issues: first, we can interpret two apparently opposite directions of morphological change as different consequences of the same triggering phenomenon; second, we can accommodate two outlying samples as resolvable expressions of the tapering morphotype, not as taxonomic anomalies. Figure 9 portrays the unusual morphologies of the two dwarfs. Note also (see appendix for more details), the key mean values in the two dwarfed samples for this interpretation. The subfossil smokestack has (at 2.70) the third largest height/width ratio among South Caicos samples, and (at 7.2) a mean whorl number only slightly below average. The Sand Cay "double whammy" has (at 2.20) by far the squattest shell of Turks Island forms, and (at 6.6) by far the smallest number of whorls.

B) Covariances of the Tapering Morphospace

The three axes of Figure 7 include 91.5% of all information, distributed as 25.6 on axis 1, 30.1 on axis 2, and 35.8 on axis 3. Table 4 presents the matrix of factor scores

for projections of variables upon these axes; we shall discuss the associations by decreasing information content of axes.

We recognize the third axis covariance from its similar expression in Table 3. The roughly equal projections for basic dimensions of the adult shell identify this axis as an expression of overall shell size (in Table 3, standardized whorl sizes covary with the raw measures of final size. Here they do not, reflecting the more common pattern of non-association between these two sets in *Cerion*).

Loadings of samples upon the third axis (Fig. 7) affirm this interpretation. This axis makes little distinction among islands, as each island harbors populations spanning a broad range of size. (Lability in size is characteristic of *Cerion*. All previous authors who sought biogeographic pattern with standard techniques of uni- and bivariate biometry were misled, by the large range of size *within* each region, to affirm a lack of distinctness between regions (see, for example, Hummelinck, 1940 and DeVries, 1974 on *C. uva*, corrected by Gould, 1984a. Multivariate techniques have revealed the basis in covariance sets for regional differences easily obscured by large variation in shell size). South Caicos samples, for example, span the entire range of third axis loadings. The generally larger shells of Grand Turk (45–100th percentile among all samples for length, and 51–86th for width) are distinguished by their higher loadings from the smaller shells of Providenciales (20–53rd percentile for length, 15–44th for width).

The second axis is crucial to our interpretation of the tapering morphotype, because it arrays each island in its own subfield, while ordering the Caicos islands in proper geographic sequence (see next subsection where we use this fact as the key for our taxonomic conclusion). Its covariances (Table 4) record a single and sensible pattern. Standardized whorl sizes are all prominent with heights for protoconch and fourth whorl (0.519 and 0.514) greater than widths (0.398 and 0.207). The only other strong values are for height/width ratio of the adult shell (a consequence of growing whorls higher than wide), and for ribs on the first whorl, a correlation that we have never before detected in *Cerion*. Note that this association records but one of the two major developmental pathways to slender shells—the other, and much more common, being simple addition of whorls (as discussed on p. 335). Samples from Providenciales load highest on this axis, South Caicos lowest. The percentile ranges of key variables fit this interpretation. Providenciales samples lie well above average in height/width ratio (64–84th percentile), but *below* in whorl number (27–34th percentile), indicating that relatively slender shells arise by growing high, not more, whorls.

The first axis records no major separation among islands. All high values are for South Caicos samples, but others from this island share lower values with populations from other islands. Turks Island samples are consistently low. The covariance ex-

TABLE 4. MATRIX OF FACTOR SCORES FOR THREE-AXIS SOLUTION OF ALL *C. REGINA* SAMPLES EXCLUDING THE SAND CAY DWARFS.

Measure	Axis 1	Axis 2	Axis 3
1. PROWID	−0.029	0.398	−0.053
2. FOURWID	0.005	0.207	0.173
3. NUMWHO	−0.002	0.046	0.244
4. RIBDENS	0.092	0.267	0.016
5. LENGTH	−0.071	0.093	0.334
6. WIDTH	−0.059	0.062	0.321
7. PROHT	−0.144	0.519	−0.056
8. FOURHT	−0.008	0.514	−0.140
9. FRSXHT	0.307	0.096	0.051
10. UMBWID	−0.070	0.021	0.372
11. LIPWID	0.069	0.044	0.162
12. LIPTHK	0.136	0.025	0.163
13. APHT	−0.053	0.013	0.328
14. APWID	−0.010	0.005	0.286
15. APROT	−0.023	0.043	0.341
16. EC	0.084	0.038	0.210
17. FA	0.391	0.188	−0.084
18. APTILT	−0.058	−0.016	0.249
19. WEIGHT	0.175	0.161	0.118
20. HWRATIO	0.352	0.237	−0.022
21. PRORAT	0.644	−0.156	−0.021
22. FOURRAT	0.321	−0.145	0.207

pressed in factor scores records a fundamental rule of *Cerion*'s growth, but one that we have not detected so clearly in our studies of northern Bahamian *Cerion*.

Consider the pattern in factor scores. Shells begin with low protoconch heights and average widths, yielding a relatively flat nucleus (width/height ratio of the protoconch scores maximally at 0.644). As the shell approaches middle growth, superficial expectations are subverted. Despite the initial advantage in width (still maintained at the fourth whorl, with width/height ratio scoring at 0.321), height asserts itself more and more prominently as the shell grows. Note the continual increase in scores for successive heights: −0.144 for the protoconch, −0.008 for the fourth whorl, and 0.307 for fourth-sixth whorl height. Thus, *early* widths are correlated with *later* heights (not later widths); or, in other words (and now interpreting), shells that begin quite flat compensate later by speeding up growth in height, and height compensation increases continually during middle growth.

We have noted this correlation of early widths with later heights again and again in our studies of land shells, not only in *Cerion* (Gould and Woodruff, 1978, 1986), but also in *Poecilozonites* (Gould, 1969b)—but its interpretation as compensation (keeping final dimensions within a limited range) had previously eluded us. We detect this pattern now because southern Bahamian *Cerion* should record it better. All *Cerion* with flat tops grow parallel-sided (or even width-*decreasing*) shells later in ontogeny, while shells that begin with a triangular top tend to maintain a gentle increase in width throughout growth. We have called the chief morphotype of the southern Bahamas "tapering" because most populations maintain a basic triangularity throughout growth. Yet the same tapering morphotype also includes the most initially flat-topped and later parallel-sided of all Bahamian *Cerion* (*C. malonei* on Long Island, populations of *C. columna* on Inagua, though the phenomenon reaches its extreme expression in species of the Cuban *C. dimidiatum* complex). This transition from triangular throughout growth to first flat-topped and then parallel-sided represents the range of expression for this first-axis covariance set. (We know, from a hybrid zone in Cuba, that direct transitions along this gradient occur, see Galler and Gould, 1979.) We had not detected this pattern in the northern Bahamas because the basic contrast between ribby and mottled morphotypes in this region expresses only a small segment of this range, while the full spate lies recorded among populations of the tapering morphotype.

We can now understand how this compensatory covariance orders populations of the Turks and Caicos. As with variation in size (third axis), all islands display a large range of loadings upon this axis, and few inter-island distinctions can be made. But Grand Turk samples are distinct in their high protoconchs (low width/height ratio from 2.04–2.33), while South Caicos populations tend to be flat-topped (range of 2.26–2.60, with only 1 sample of 20 below the maximal Grand Turk value of 2.33, and eight of 20 above 2.50). Yet this initial distinction is compensated in later growth as the early flatness of South Caicos shells engenders later exaggeration of height—for the final height/width ratios scarcely differ (range of 2.49–2.63 for Grand Turk and 2.44–2.78 for South Caicos).

C) A Taxonomic Decision: All Tapering Populations Belong to the Single Species, *Cerion regina*

The geographically localized and morphometrically restricted *C. blandi* and *C. lewisi* pose no taxonomic problems. They are distinct, immigrant forms and merit recognition as species (despite the hybridization of *C. blandi* with indigenous tapering populations, a pervasive phenomenon among *Cerion* taxa).

The problem of the Turks and Caicos *Cerion* fauna (both in the existing literature and in our morphometric data) centers upon widely varying populations of

the indigenous tapering morphotype. Can they all be gathered under one species, *C. regina* by priority (and a lovely name as "queen *Cerion*"), or have they differentiated to an extent meriting taxonomic subdivision? Three separate issues confront us: the status of morphometric outliers (the two dwarf samples), the validity of existing names in the literature, and the order and extent of morphometric variation among our measured samples.

We have already shown (see p. 336) that the dwarf samples, although morphometrically distant from the major clusters, are products of single transformations (and their correlated effects) noted again and again in dwarfed *Cerion* populations continuous with, and showing no sign of differentiation from, adjacent populations of normal size (Gould, 1984b; Gould and Woodruff, 1986; Woodruff and Gould, 1980).

Four species names exist in the literature for tapering forms from the Turks and Caicos. Clench (1961) had already synonymized the two Turks Island forms by sinking *C. incanoides* Pilsbry and Vanatta, 1895 into *C. regina* Pilsbry and Vanatta, 1895. We do not challenge this decision.

Do paratype populations of the remaining two species, *C. utowana abbotti* and *C. caicosense*, provide any evidence for valid distinction? *C. utowana abbotti* is easily dismissed by our morphometric evidence. As Figure 7 demonstrates, we include three samples named *C. utowana abbotti* by Clench (who described the taxon in 1961)—one from South Caicos (the paratypes), one from East Caicos and one from Long Cay on the Turks Bank. The South and East Caicos samples plot within the arrays of other samples from their island named *C. caicosense* by Clench. We have no other samples from Long Cay, but Clench's *C. utowana abbotti* lies within the morphospace of *C. caicosense*. We may therefore synonymize *C. utowana abbotti* into whatever status *C. caicosense* deserves.

The paratype sample of *C. caicosense* (Fig. 7) lies at the periphery of the South Caicos array (as formally designated taxa so often do), but clearly not apart from it. This population also has no claim for separation beyond its general membership in the South Caicos field.

We must, finally, consider the tapering morphospace itself (Fig. 7). The main argument for taxonomic distinction would lie in the separation of the South Caicos and Turks Island fields, for these are the type areas of the two available taxa, *C. regina* (Turks Island) and *C. caicosense* (South Caicos). Indeed, in the full morphospace of Figure 5, South Caicos lies as far from Grand Turk as the other legitimate taxa, *C. blandi* and *C. lewisi*, lie from each other.

The key to a proper taxonomy for the tapering morphotype lies in how samples from the other islands fit into the morphospace. If we find clear and separated clusters representing the geographically distinct Turks and Caicos banks, then we might admit the two existing names at some formal level. However, all representations of the morphospaces (Figs. 5–8) show the same pattern: populations from other islands of the Caicos Bank fully and continuously fill in the space between separated South Caicos and Turks Island clusters. We therefore find continuity in morphological distribution over the entire recorded range of the tapering morphotype, and no basis for taxonomic distinctions on this account.

But the pattern of intermediacy also speaks for unification through another aspect of its ordering. Our total array (Figs. 6 and 7) contains multiple samples from four islands of the Caicos Bank—Providenciales (3), Grand Caicos (3), East Caicos (4) and South Caicos (16). A comparison with the geography of islands (Fig. 1) shows that each island occupies a discrete part of the morphospace and, more importantly, that the four domains are arrayed in perfect geographical order from South Caicos through East and Grand to the most distant Providenciales (see Fig. 10). Moreover, the equally restricted mor-

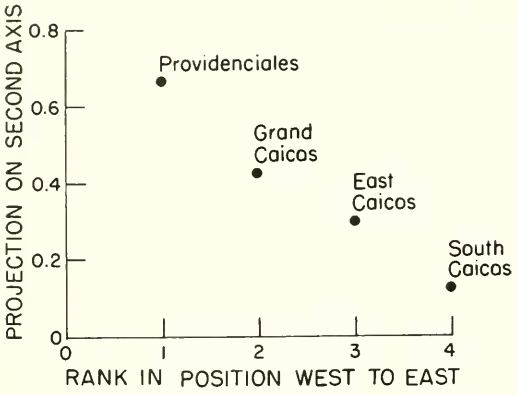

Figure 10. Plot of average projection of all samples upon the second axis versus rank in position along the north edge of the Caicos Bank, west to east.

phological domain of Grand Turk lies within this array.

We also know the basis in covariance for this clinal distribution (see last subsection): an increase in size of standardized early whorls towards Providenciales, with height increasing more than width, leading from the relatively flat-topped populations of South Caicos to the more slender and larger-whorled populations of Providenciales (see Fig. 3). This cline (Fig. 10) records standardized whorl sizes and their consequences for shape, not adult shell size; the Providenciales samples are, if anything, slightly smaller in size than most South Caicos populations, while each island forms a large and nondistinctive array for overall size (Grand Turk shells tend to be large, but one sample lies below the percentile means for adult length and height among tapering samples). All Caicos samples are therefore ordered by geography in a cline defined by a sensible determinant of shape and its associated covariances.

We used the same criterion of geographically ordered clinal distribution in morphology to unite a set of morphologically and geographically more distinct populations into the single species *C. striatellum* from Hispaniola to the Virgin Islands (Gould and Paull, 1977). For all these reasons, we find no basis for any taxonomic distinctions within the tapering morphotype of the Turks and Caicos islands. We therefore synonymize all previous taxa, and recognize only *C. regina* as the appropriate name for the indigenous *Cerion* of the Turks and Caicos islands. The *Cerion* fauna of this geographic outlier of the southern Bahamas therefore includes three species, the native *C. regina* from all major islands, and two restricted immigrants, *C. blandi* from Salt Cay, Turks Bank, and *C. lewisi* from several islands on the northwestern Caicos Bank. The indigenous species belongs to the common morphotype of its general region, while the two immigrants, both fortunately quite distinctive in morphology, have recognizable sources on nearby Cuba.

D) Genetics

This taxonomic conclusion, based solely on conchological and biogeographic data, is strongly supported by our population genetic survey. Although we cannot assess the genetic status of *C. blandi* and *C. lewisi*, we can document the strong genetic relatedness of *C. regina* from Providenciales and South Caicos on the Caicos Bank and Grand Turk on the Turks Bank.

Eight of the 16 genetically interpretable loci were monomorphic in the 17 samples studied: *Crp*, *Es-1*, *Es-6*, *Ldh-2*, *Mdh-2*, *Pgm-1*, *Pr-1*, *Sod-1*. The frequency of the various alleles at the seven polymorphic loci are shown in Tables 5–7. Three loci were diallelic (*Gapd*, *Gpi*, *Pgm-2*); *6Pgd* had three alleles, and three loci had up to four alleles segregating (*Es-2*, *Aat*, and *Mdh-1*). Data for acid and alkaline phosphatases are not reported as the results were uninterpretable. *Ldh-1* data are excluded as only three samples (758–760) were studied; they share a common allele, a second allele was segregating at 759–760, and a third allele was detected at 760.

Tables 5–7 show that the Grand Turk sample (766) is strikingly different from the others in its level of genetic variability. In contrast to the moderate levels of variation seen in all Caicos Bank samples the

TABLE 5. VARIATION IN ASPARTATE AMINOTRANSFERASE AND ESTERASE-2 ALLELE FREQUENCY.

Sample	$\bar{N}$*	$Aat^{1.2}$	$Aat^{1.0}$	$Aat^{0.7}$	$Aat^{0.4}$	$Es\text{-}2^{1.2}$	$Es\text{-}2^{1.1}$	$Es\text{-}2^{1.0}$	$Es\text{-}2^{0.9}$
					Providenciales				
770	29	0.05	0.95	—	—	—	—	1.00	—
772	31	0.00	1.00	—	—	—	0.03	0.97	—
					South Caicos				
753	32	0.03	0.97	—	—	—	—	1.00	—
757	29	0.10	0.90	—	—	—	—	1.00	—
754	32	0.03	0.97	—	—	—	—	1.00	—
758T	23	0.04	0.96	—	—	—	—	1.00	—
758	32	0.10	0.90	—	—	—	—	1.00	—
759	29	0.07	0.91	—	0.02	—	—	1.00	—
760	31	—	1.00	—	—	—	—	1.00	—
761	29	—	1.00	—	—	—	—	1.00	—
762	32	—	1.00	—	—	—	0.03	0.97	—
764	31	—	0.98	0.02	—	0.02	0.02	0.96	—
749	32	—	1.00	—	—	—	—	0.94	0.06
750	32	—	0.94	0.06	—	—	—	0.98	0.02
751	32	—	0.97	0.03	—	—	—	1.00	—
752	32	—	1.00	—	—	—	—	0.98	0.02
					Grand Turk				
766	31	—	1.00	—	—	—	—	1.00	—

* $\bar{N}$ = mean sample size per locus.

31 snails from Grand Turk were isogenic at all loci studied. However, as the Grand Turk sample is fixed for the common allele segregating at each polymorphic locus on South Caicos it is clearly closely related to the Caicos populations. We hypothesize that the Turks Island populations are descendants of a very few colonists from the Caicos Bank that, by chance, failed to carry or subsequently lost, the less frequent alleles of the source population. Such a scenario is in keeping with the traditional view that much interisland dispersal of *Cerion* results from the vagaries of hurricane transportation. At least one other species, *C. incanum*, is known to be isogenic in part of its range (Woodruff and Gould, 1987). In the lower Florida Keys four samples of 30 snails each were all monomorphic at 17 loci. One hundred km further north at Key Biscayne adjacent to the Florida mainland three samples showed variation at 1–2 loci.

The variation in allele frequencies reported in Tables 5–7 were used to establish the mating system and population structure of *C. regina*. The allele frequency estimates are reasonably robust as sample sizes were typically more than 30 individuals. A measure of the replicability of these estimates is provided by the comparison of data for samples 758T and 758; allele frequency differences at the three polymorphic loci (*Aat*, *Mdh-1*, *6Pgd*) are insignificant. (Note also that both samples were treated morphologically and found indistinguishable, see Figs. 14, 16.)

We tested genotype frequency data for each variable locus in each sample for significant deviation from values expected under panmixia. In only three of 67 χ^2-tests did the probability that the frequencies were in Hardy-Weinberg equilibrium fall below 0.05. In these cases, however, the simple χ^2-tests were inappropriate and when exact probabilities were calculated these were all >0.15. We conclude that *C. regina*, an anatomical hermaphrodite, is outbreeding at random on Providenciales and South Caicos. This conclusion was supported by the calculation of Wright's index, F_{is}, the inbreeding coefficient of an

TABLE 6. VARIATION IN GLUCOSE PHOSPHATE ISOMERASE, GLYCERALDEHYDE DEHYDROGENASE AND MALATE DEHYDROGENASE-1 ALLELE FREQUENCY.

Sample	$Gpi^{1.4}$	$Gpi^{1.0}$	$Gapd^{1.0}$	$Gapd^{0.7}$	$Mdh\text{-}1^{1.2}$	$Mdh\text{-}1^{1.0}$	$Mdh\text{-}1^{0.8}$	$Mdh\text{-}1^{0.6}$
				Providenciales				
770	—	1.00	0.97	0.03	0.02	0.69	0.03	0.26
772	0.03	0.97	1.00	—	—	0.84	—	0.16
				South Caicos				
753	—	1.00	0.95	0.05	0.02	0.76	0.02	0.20
757	—	1.00	1.00	—	—	0.62	—	0.38
754	—	1.00	1.00	—	—	0.72	0.02	0.26
758T	—	1.00	1.00	—	—	0.50	—	0.50
758	—	1.00	1.00	—	—	0.47	0.03	0.50
759	0.02	0.98	1.00	—	0.04	0.60	0.04	0.32
760	0.02	0.98	1.00	—	—	0.58	—	0.42
761	—	1.00	1.00	—	—	0.68	0.02	0.30
762	0.02	0.98	1.00	—	—	0.91	—	0.09
764	0.02	0.98	1.00	—	—	0.94	—	0.06
749	—	1.00	0.92	0.08	—	0.83	0.14	0.03
750	0.03	0.97	0.86	0.14	—	0.92	—	0.08
751	0.02	0.98	0.94	0.06	—	0.88	—	0.12
752	0.02	0.98	0.86	0.14	—	0.72	—	0.28
				Grand Turk				
766	—	1.00	1.00	—	—	1.00	—	—

individual relative to its sample. The mean F_{is} for all seven polymorphic loci in all samples was 0.036 indicating that the snails sampled could all have been drawn from a single outbreeding metapopulation. Finally, we calculated coefficients of heterozygote deficiency for all variable loci and again found no significant heterozygote deficiency or excess in the samples. All three approaches indicate that *C. regina* is amphimictic on the Caicos Bank.

These tests cannot, of course, be applied to the monomorphic snails of Grand Turk (sample 766). It seems most unlikely that their isogenicity is due to a radical change in reproductive strategy—from outbreeding to self-fertilization—as the ability to do so is unknown in *Cerion*. Instead, as hypothesized herein, we attribute their genetics to a founder effect associated with the successful colonization of the Turks Bank by a few snails from the Caicos Bank. The study of additional samples from this, the most isolated of the Bahamian banks, should clarify this situation.

The remaining 16 samples representing 15 populations from Providenciales and South Caicos on the Caicos Bank are all moderately variable (Tables 5–7). The mean number of alleles per locus $\bar{A} = 1.3$ (range 1.2–1.5), the mean proportion of polymorphic loci $\bar{P} = 0.28$ (range 0.20–0.40), and the mean individual heterozygosity $\bar{H} = 0.06$ (range 0.05–0.09). The typical sample is thus polymorphic at four of the 15 loci and the most variable sample (750) at six loci. These levels of intrapopulation variability in *C. regina* are very similar to those determined for other well-characterized species of *Cerion* (Gould and Woodruff, 1978, 1986; Woodruff, 1975; Woodruff and Gould, 1987). Although these estimates of genetic variation are minimum estimates (as they are based on single-gel electrophoresis) they probably reflect 80% of the true variation at these structural gene loci (Ayala, 1983; Selander and Whittam, 1983).

The finding that *C. regina* is amphimictic permits us to use Nei's (1978) unbiased measures of multilocus genetic identity (I) and genetic distance (D) to

TABLE 7. VARIATION IN PHOSPHOGLUCOMUTASE-2 AND 6-PHOSPHOGLUCONATE DEHYDROGENASE ALLELE FREQUENCY AND IN OVERALL SAMPLE GENETIC VARIABILITY.

Sample	*Pgm-2*$^{1.3}$	*Pgm-2*$^{1.2}$	*6Pgd*$^{1.0}$	*6Pgd*$^{0.9}$	*6Pgd*$^{0.8}$	$\bar{A}$	*P*	$\bar{H}$
				Providenciales				
770	0.02	0.98	0.79	0.21	—	1.5	0.33	0.06
772	—	1.00	0.69	0.29	0.02	1.3	0.27	0.06
				South Caicos				
753	0.02	0.98	0.80	0.20	—	1.5	0.33	0.05
757	—	1.00	0.83	0.17	—	1.2	0.20	0.06
754	—	1.00	0.76	0.24	—	1.3	0.20	0.05
758T	—	1.00	0.68	0.32	—	1.2	0.20	0.06
758	—	1.00	0.59	0.41	—	1.3	0.20	0.09
759	0.02	0.98	0.64	0.36	—	1.5	0.33	0.08
760	0.02	0.98	0.71	0.29	—	1.3	0.27	0.07
761	0.02	0.98	0.76	0.24	—	1.3	0.20	0.05
762	—	1.00	0.56	0.39	0.05	1.3	0.27	0.05
764	—	1.00	0.55	0.43	0.02	1.5	0.33	0.05
749	—	1.00	0.84	0.16	—	1.3	0.27	0.05
750	—	1.00	0.69	0.31	—	1.4	0.40	0.06
751	—	1.00	0.66	0.34	—	1.3	0.33	0.06
752	—	1.00	0.60	0.40	—	1.3	0.33	0.08
				Grand Turk				
766	—	1.00	1.00	—	—	1.0	0.0	0.0

$\bar{A}$ = mean no. alleles per locus, *P* = proportion of loci polymorphic, $\bar{H}$ = mean individual heterozygosity per locus.

assess the overall pattern of differentiation within this species. The results show that only minor geographic differentiation has occurred, a finding concordant with the calculation of Wright's fixation index (F_{st} = 0.08). A similarity matrix (available from D.S.W.) for all pairwise comparisons of the 17 samples showed *I* values to range from 1.00 to 0.982 on South Caicos. Overall similarity is higher than this range suggests as 75% of the 136 values ≥0.995. The lowest *I* value (0.971) involved samples 758 (northeast South Caicos) and 766 (Grand Turk).

The similarity matrix can be visualized by cluster analysis. Here we present a genetic distance phenogram (where $D = -\ln I$) prepared by the unweighted pair group with averaging (UPGMA) algorithm (Fig. 11). Nei's genetic distance, *D*, a multilocus measure of intersample differences, may range between 0.00 (identity) and infinity. Within a group of sexually reproducing organisms *D* values increase with taxonomic distance. For example, only about 2% of 7,000 estimates of *D* between conspecific populations of a wide range of organisms exceed 0.10 and only 2% of 900 estimates of *D* between congeneric species fell below 0.15. Interspecific genetic distances of mammals, fish, and reptiles are typically in the range of $D = 0.3–0.5$ (Avise and Aquadro, 1982) and published results for mollusks are also generally in this range (Woodruff and Merenlender, in prep.). *Cerion* (and birds) are a little exceptional in that they show less differentiation within and between species than most other groups. Nevertheless, no *Cerion* species or semispecies are known where the interspecific *D* is less than 0.05 or the intraspecific *D* exceeds a similar value (Gould and Woodruff, 1986; Woodruff and Gould, 1980, 1987).

Given this background it is clear from Figure 11 that *C. regina* is remarkably homogenous genetically. After pairwise averaging, the greatest *D* value separating clusters of samples is only 0.01. It must be remembered that the error on such small

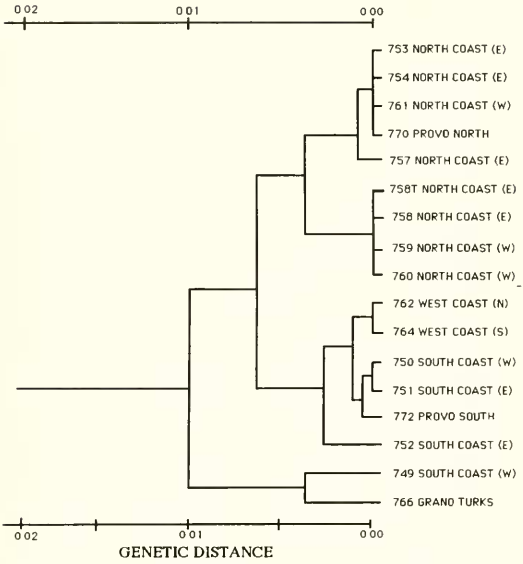

Figure 11. A dendrogram based on UPGMA clustering of 17 samples of *Cerion regina* from Providenciales, South Caicos and Grand Turk using the unbiased genetic distance (*D*) of Nei (1978). Samples are identified according to their locality number and geographic location (*PROVO* = Providenciales; *N*orth, *S*outh, *E*ast, *W*est).

branch-point estimates exceeds the *D* value itself; no great biological significance can be placed on the subclustering in Figure 11. Notwithstanding this caution, we immediately note two interesting aspects of clustering in the 17 samples. The first is that the Providenciales samples are embedded in the South Caicos cluster. Samples 770 and 772 from the north (bank-edge) and south (bank-interior) coasts of Providenciales are genetically indistinguishable from samples from South Caicos. Most interestingly, these two samples cluster with the biogeographically equivalent groups on South Caicos, i.e., 770 with the northeastern bank-edge group, 772 with the southwestern bank-interior group. (This within island patterning will be discussed in more detail in section VII.) The second significant result in Figure 11 involves Grand Turk (766): *Cerion* on this isolated island bank are indistinguishable from those of the Caicos Bank. The only distinction (manifest as $\bar{D} = 0.01$) stems directly from the fact that Grand Turk's snails are fixed for the common alleles on the Caicos Bank. There is thus no genetic evidence to support the recognition of *C. caicosense* as a separate species. Again, no special significance can be placed on specific branch-points at this level of differentiation so the clustering of sample 766 with sample 749 (southwest South Caicos) does not indicate that the Turks Bank populations were founded by this Caicos population. In fact, individual snails homozygous at all variable loci for the same alleles that are fixed on Grand Turk occur in every one of the South Caicos and Providenciales samples.

The genetic data therefore lead to the following conclusions. *C. regina* is a typical amphimictic species. Despite fragmentation of populations today on two island banks separated by the 32 km wide Turks Island Passage there is no evidence of genetic differentiation. Similarly, the populations on Providenciales and South Caicos, presumably continuous a few thousand years ago but separated today by about 100 km of water, are genetically indistinguishable. Such low levels of genetic differentiation are typical of other known species of *Cerion* and of conspecific populations generally.

E) A Note on Minor Axes and General Geometry

We have seen that the major axes of our factor analyses sort the islands into discrete groups and order them into a clinal array that supports the unification of all populations into the single species *Cerion regina*.

We have argued in previous works (Gould and Woodruff, 1978, 1986 in particular) that minor axes should not be ignored, for they may display significant biological information based on few variables in few samples (even if statistically "insignificant" in another, technical sense of the word). In the *C. regina* morphospace, most minor axes yield no general interpretation, for they capture only the peculiarities of

single samples for single measures. But the fourth axis, carrying some 10% of information, displays a coherent and interesting aspect of covariance well known from all our *Cerion* studies. Note, in Table 8, that three of the highest scores form a well-known covariance set based on whorl number and its consequences for shape—many whorls (0.390) produce a high (0.225), not a wide (0.012), shell because later whorls, in the second allometric phase, add height but little or no width, leading to large height/width ratio of the adult shell (0.416).

If we now consider the two highest negative scores, we note standardized whorl sizes of the early shell—fourth whorl width at −0.277 and fourth to sixth whorl height at −0.248. This negative association is the pervasive constraint—we call it the constraint covariance—that we have identified in all *Cerion* studies (see particularly Gould and Paull, 1977; Gould and Woodruff, 1978). If a shell begins by growing larger than average whorls, it will necessarily grow fewer of them to reach the same final size. Thus, when final sizes fall in a limited range, we find negative associations between whorl numbers and measures of standardized whorl sizes. This constraint holds particular interest because it imposes forced correlations for basic shape as well. The shell with small and many whorls will be slender and parallel-sided, while the alternative with fewer, larger whorls will be squatter and continually increasing in width. These forced correlations arise because shells, in the second allometric phase, add height but little or no width. The more whorls added in this phase, the more slender the adult shell (Gould, 1984b).

When we plot (Fig. 12) all samples onto this constraint axis, we note a different pattern. High values do not mark any geographic location, but rather pluck out a sample or two from each major place; the five highest loadings include two for East Caicos and one each for Grand Caicos, Providenciales and Grand Turk. (Two East Caicos samples are high, but the other two from this island are lower than average.) The constraint covariance is a pervasive rule of growth within all *Cerion*, not the unique association of a single place. Thus, it can "attract" samples from any region that happen to grow (in this case) with small whorls, and thereby develop with the forced correlations so implied. Finally, we note in Figure 13 that the constraint covariance acts in the same way upon the full morphospace, selecting one or two samples from all taxa and regions by virtue of smaller than average whorls that can occur in *any* taxon or region, and then carry their train of enjoined consequences with them.

TABLE 8. FACTOR SCORES ON FOURTH AXIS (12.6% OF INFORMATION) OF AN ANALYSIS FOR ALL TAPERING SAMPLES EXCEPT FOR SAND CAY DWARFS.

Measure	Axis 4
1. PROWID	−0.210
2. FOURWID	−0.277
3. NUMWHO	0.390
4. RIBDENS	0.442
5. LENGTH	0.225
6. WIDTH	0.012
7. PROHT	0.164
8. FOURHT	−0.097
9. FRSXHT	−0.248
10. UMBWID	0.204
11. LIPWID	0.138
12. LIPTHK	0.030
13. APHT	0.132
14. APWID	0.099
15. APROT	0.272
16. EC	−0.000
17. FA	−0.108
18. APTILT	0.243
19. WEIGHT	−0.084
20. HWRATIO	0.416
21. PRORAT	−0.115
22. FOURRAT	−0.031

VII. Covariation at Level Three: Does Order Still Reign Within Islands?

Descending now to the finest level of among-sample relationships, we shall consider the distribution of samples for a single island, our most completely collected

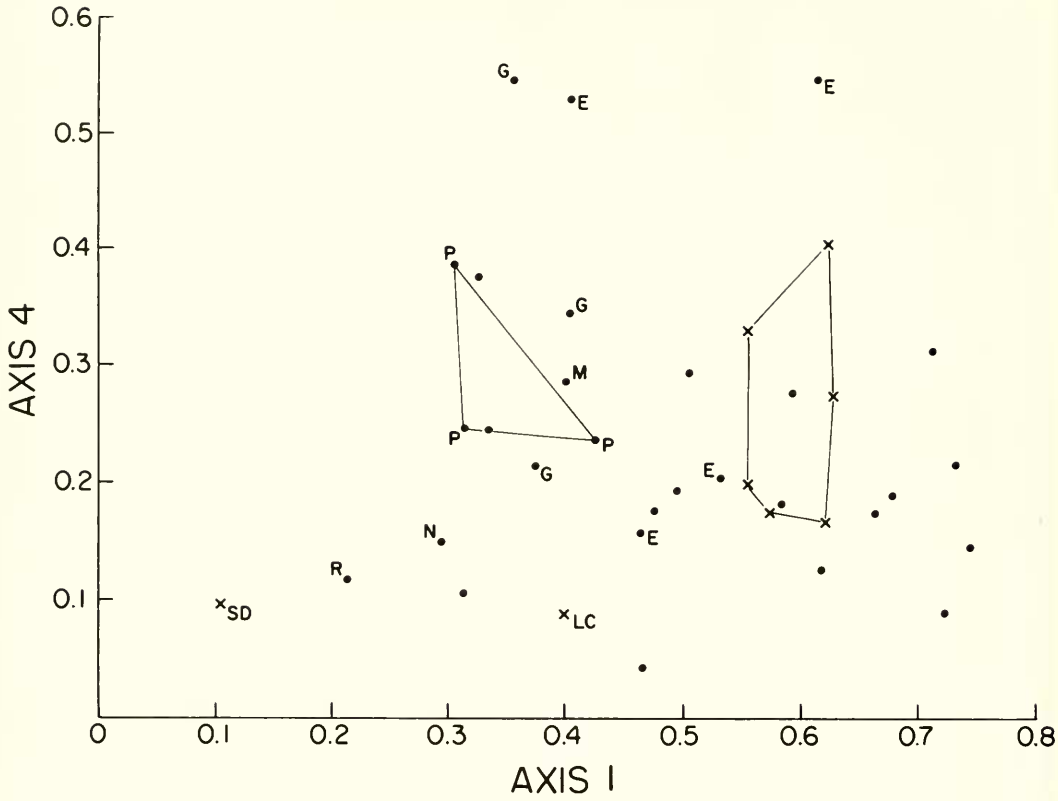

Figure 12. Loadings of mean vectors for *C. regina* samples upon first and fourth axes. Symbols as in Figure 5 except Caicos Bank samples are dots and Turks Bank samples are crosses. Note that the fourth axis, expressing the geometrically necessary negative covariation of whorl size and whorl number, does not identify any particular region, but isolates a few samples from several regions.

South Caicos, within their own morphospace. We have shown (both here and in all our *Cerion* studies of other island groups) that geographic variation *within* islands also displays ordered pattern rather than random arrays. (Thus, older claims for crazy-quilt distributions are false at all levels—from the highest of taxonomic separation between major banks to the finest of minor differentiation within single taxa on single islands.) We have found repeated order based on recurrent habitat (Gould, 1984a on windswept platforms versus secluded valleys, and on limestone or volcanic substrates in *C. uva*), and on simple geographic contiguity [distinction of Treasure Cay samples of *C. bendalli* on Abaco (Gould and Woodruff, 1978); or of offlying cay populations of *C. glans* on New Providence (Gould and Woodruff, 1986)]. We now report a similar coherence for tapering samples on South Caicos as well.

The five-axis solution for South Caicos samples seems to capture all important dimensions of covariance, with no subsequent axis including even one percent of information. We plot, as Figure 14, the loadings of all South Caicos samples (excluding the subfossil dwarf outlier, 765, discussed earlier) upon the two axes explaining most information (axis 1 at 37.9% and 3 at 23.9%; no other axis exceeds 15%). A comparison of these loadings with geo-

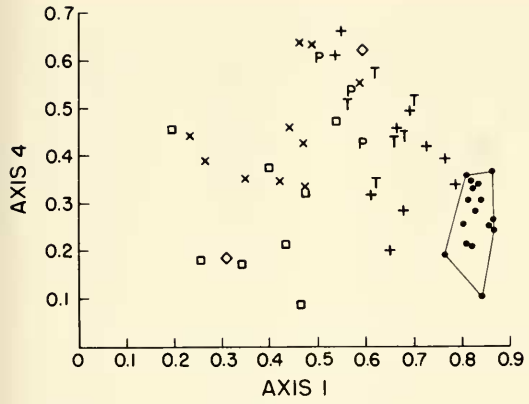

Figure 13. Loadings of mean vectors for all samples upon first and fourth axes. Note, as in Figure 12, that the fourth axis isolates some samples from all regions and taxa. As in Figure 5, crosses are *C. blandi* and squares are *C. lewisi.* For *C. regina* dots are South Caicos; plusses are other Caicos islands; T are Grand Turk; and diamonds are other Turks Bank samples.

graphic position (Fig. 15) shows that samples plot into the South Caicos morphospace largely by geographic location; subregions of this small island can be iden-

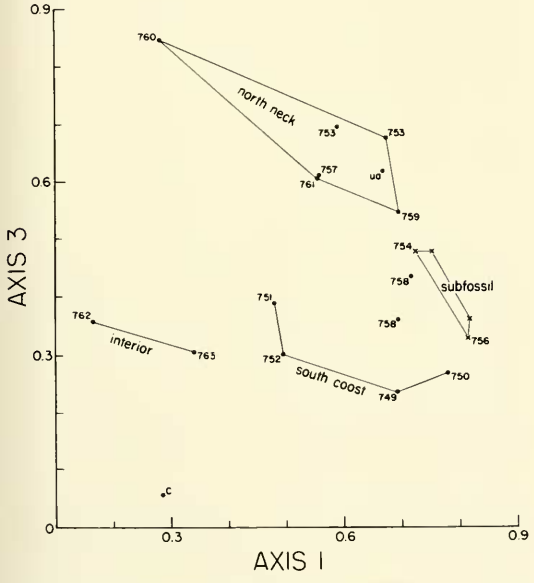

Figure 14. Loadings for South Caicos samples only. Dots are modern samples, crosses are fossils. All points include our collection number (see Fig. 14) except for the two paratype samples collected previously: c is *C. caicosense*; ua is *C. utowana abbotti.* Note good separation by region and time, even on this very small island.

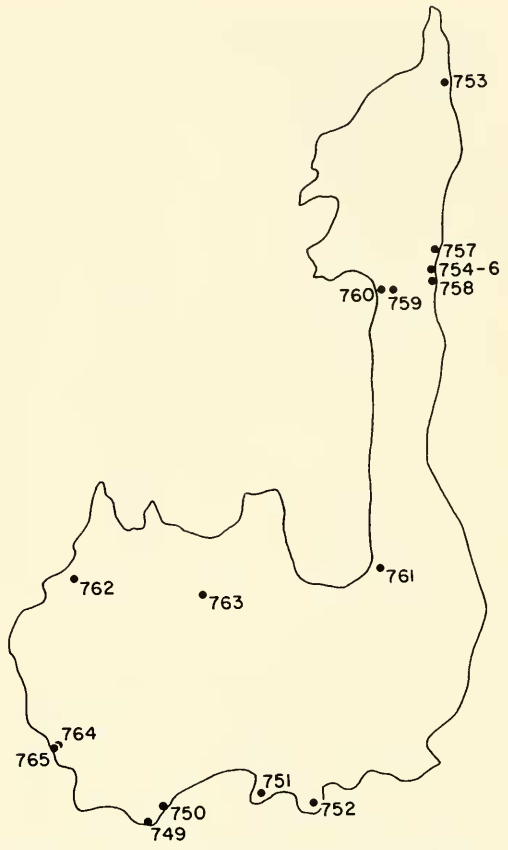

Figure 15. Outline map of South Caicos showing location of our samples.

tified by morphology. In addition, we gain some confidence in our methods of measurement by noting that for two locations with two samples each (753 and 758), the two loadings for each place are adjacent. (In each location, snails in one sample came from a single tree, and the other sample from surrounding grass and bushes.)

The first axis distinguishes subfossil samples by high loadings and the two interior samples (at the airstrip) by low loadings. The third axis contrasts samples from the northern neck of the island (high loadings) with central and southern samples. Taken together, we may identify four broad temporal and geographic domains (not distinct clusters since they overlap, but not random arrays because they do not interpenetrate):

TABLE 9. SCORES OF FIVE-AXIS SOLUTION FOR SOUTH CAICOS SAMPLES.

Measure	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
1. PROWID	0.331	−0.043	−0.011	0.061	0.156
2. FOURWID	0.260	0.025	0.142	0.155	0.320
3. NUMWHO	0.079	−0.031	0.170	−0.365	−0.133
4. LENGTH	0.226	−0.070	0.096	−0.091	−0.038
5. WIDTH	0.206	−0.114	0.171	−0.031	0.156
6. PROHT	0.380	−0.076	−0.209	−0.286	−0.016
7. FOURHT	0.403	0.473	−0.124	0.306	−0.015
8. FRSXHT	0.341	0.024	0.052	0.233	0.170
9. UMBWID	0.030	0.053	0.427	0.052	−0.047
10. LIPWID	0.240	0.063	0.092	0.078	−0.292
11. LIPTHK	0.167	−0.030	0.066	−0.066	−0.113
12. APHT	0.230	−0.082	0.146	−0.008	−0.044
13. APWID	0.188	−0.096	0.178	−0.046	0.040
14. APROT	0.192	−0.019	0.312	−0.072	−0.214
15. EC	0.122	−0.145	0.014	−0.371	0.229
16. FA	0.056	0.346	−0.255	−0.475	0.391
17. APTILT	−0.108	0.005	0.486	−0.129	−0.126
18. HWRATIO	0.076	0.409	−0.031	−0.397	−0.448
19. PRORAT	−0.209	0.638	0.330	0.066	0.235
20. FOURRAT	−0.094	−0.103	0.308	−0.196	0.416

subfossils (all from the northern neck), modern samples from the northern neck, the south coast, and the western interior at the airstrip. We were surprised (and pleased) to find these distinctions on such a small island with populations in broad contact. The type sample of *C. caicosense*, with high loadings on the second axis (see below), plots with low loadings on both axes of Figure 14.

The patterns of covariance revealed by factor scores help to explain these patterns among samples (Table 9). We recognize, in the nearly uniform scores for all measures of size (final and whorl-standardized in this case) on the first axis (37.9%), the signature of general size that we have identified at all levels in this study. We can therefore identify the basis for distinction of the large subfossils. More important, we now note for the first time in the tapering morphotype the same basic pattern that sets relationships of size in the ribby and mottled morphotypes of the northern Bahamas: large and thick shells of exposed coasts contrasting with smaller and thinner shells of calm coasts and island interiors. Note this contrast for divisions *within* both the southern and northern domains on South Caicos. In the north, the samples of the exposed, bank-edge east coast (753, 758) load high, and the calm, bank-interior west coast low (760). In the south, coastal samples are high (749–752), interior samples low (762–763).

The second axis (14.4% of information), with high loadings only for the *C. caicosense* paratypes and two southern samples (752, 762) expresses an aspect of the central covariance regulating *Cerion*'s shape, and discussed above (p. 337): the play-off between initial flatness and later acceleration in height (leading to an apparent contrast that actually represents two expressions of the same rule at opposite extremes of its action—a shell roughly triangular throughout and continually expanding in width, versus a flat-topped shell compensated later by rapid growth in height to produce a parallel-sided adult shell). *C. caicosense* is, apparently, not a valid taxon, but the name given to one end of this continuity in a key morphogenetic rule—the flattened nucleus and later compensation in height most characteristic of South Caicos' unique samples (see Figs. 5–

8). All high scores on the second axis fit this interpretation [initial flatness (width/height ratio of the protoconch at 0.638), followed by compensatory height (fourth whorl height at 0.473, and last whorl height FA at 0.346), leading to a high-spired shell (final height/width ratio at 0.409)].

The third axis (23.9%), the other major basis of sensible distinctions among South Caicos samples, captures another aspect of this key covariance in shape. Initial flatness, this time of both protoconch (measure 19 at 0.330) and fourth whorl (measure 20 at 0.308), is compensated by continually increasing assertion of standardized height (smooth increase of scores for measures 6–8 from −0.209 to −0.124 to 0.052). In addition (and if related by developmental architecture, we do not know how), we find correlated high scores for the three measures of accentuated change of shape in the adult aperture, the third allometric phase of *Cerion* (apertural rotation, measure 14, at 0.312; apertural tilt, measure 17, at 0.486; and umbilical width, measure 10, increasing as the aperture tilts away, at 0.427). Thus, samples with high loadings on this axis have strong apertures and flattened tops, followed by later compensatory growth in height. This distinction sets the primary contrast between northern and southern samples on South Caicos.

The fourth and fifth axes (14.7 and 6.6% of information) do not make broad geographic distinctions among samples. Both emphasize the standardized sizes of early whorls in their covariances, and we find, as we have before (see Gould and Paull, 1977, for example), a contrast between heights (fourth axis) and widths (fifth axis). Other high scores associate sensibly with these standardized sizes according to the principal constraint that we have identified in *Cerion* (discussed in section VI E): under limitations upon final shell size, large early whorls imply fewer total whorls, leading to forced correlations in final shape, especially the building of greater height along the many and small whorled pathways. Note the negative association of whorl number (−0.365) and final height/width ratio (−0.397) with high scores for standardized heights (0.306 for fourth whorl, 0.233 for fourth to sixth whorl) on axis 4. The same pattern repeats on the fifth axis, where strong standardized widths (0.156 for the protoconch, 0.320 for the fourth whorl) associate negatively with whorl number (−0.133), final height/width ratio (−0.448), and also yield in this case, a flattened top produced by the strong early widths (unmatched by heights): 0.235 for width/height of protoconch, and 0.416 for width/height at the fourth whorl.

The triangular, three axis solution collapses this covariance by amalgamating general size with one aspect of the key shape covariance (the flat-top later-height principle) on the first axis (now 55.8% of information), according (as in the 5-axis solution) another aspect of this key shape covariance to the second axis (now 19.2%), and joining the fourth and fifth axes into a single axis (the third at 17.5%) by incorporating both standardized heights and widths, and recording the chief constraint of negative interaction between large early sizes and few total whorls. These covariances are expressed in Table 10. This arrangement divides the determinants of form within the South Caicos morphospace into its three major principles—size on the first axis, the major covariance determining variation in shape on the second (the compensation of initial flatness by later growth in height), and the major constraint forcing correlations among characters on the third (negative association between whorl size and whorl number under limitations upon the range of final shell size).

The triangular plot of sample loadings (Fig. 16) makes the same distinctions as Figure 14, with tighter clustering around the now more dominant first axis, and greater separation of the *C. caicosense* paratypes on the second axis, and the interior samples (762–763) on the third. This figure also records an important point about

TABLE 10. SCORES OF THREE-AXIS SOLUTION FOR SOUTH CAICOS SAMPLES.

Measure	Axis 1	Axis 2	Axis 3
1. PROWID	0.302	0.097	0.172
2. FOURWID	0.363	0.124	0.183
3. NUMWHO	0.127	−0.061	−0.375
4. LENGTH	0.230	−0.029	−0.063
5. WIDTH	0.315	−0.048	0.005
6. PROHT	0.197	0.129	−0.029
7. FOURHT	0.166	0.527	0.260
8. FRSXHT	0.333	0.126	0.265
9. UMBWID	0.230	−0.098	−0.183
10. LIPWID	0.143	0.007	−0.025
11. LIPTHK	0.140	−0.025	−0.070
12. APHT	0.258	−0.062	−0.019
13. APWID	0.269	−0.071	−0.048
14. APROT	0.261	−0.113	−0.215
15. EC	0.197	0.001	−0.174
16. FA	−0.025	0.543	−0.218
17. APTILT	0.142	−0.202	−0.389
18. HWRATIO	−0.139	0.296	−0.493
19. PRORAT	−0.017	0.444	−0.245
20. FOURRAT	0.229	−0.081	−0.186

taxonomic practice. We see that the invalid names *C. utowana abbotti* and *C. caicosense* are not geographically defined areas of microdifferentiation, but extreme expressions (within the morphospace) of tendencies in covariance common to the entire sample—*C. utowana abbotti* by size, *C. caicosense* by the major shape covariance set.

Thus, variation within South Caicos is both geographically coherent and expressed along the major lines of developmental channeling in *Cerion*—a fine example of the interplay (not antithesis) between themes of constraint and adaptation.

A similar pattern of geographic coherence can be seen in the genetic data for the 13 populations sampled on this small island. Figure 11 clearly shows two clusters of samples: those from the northeast of the island and those from the south and west coasts. (Note that the populations sampled are the same as those discussed morphometrically except for the omission of 763 and the addition of the west coast 764.) Inspection of Tables 5–7 reveals the minor differentiation underlying this dichotomy. The northern end of the island is characterized by higher frequencies of $Aat^{1.2}$, $Mdh\text{-}1^{1.2}$, $Mdh\text{-}1^{0.8}$, $Mdh\text{-}1^{0.6}$ and $Pgm\text{-}2^{1.3}$. The southern and western populations have higher frequencies of $Aat^{0.7}$, $Es\text{-}2^{1.2}$, $Es\text{-}2^{1.1}$, $Es\text{-}2^{0.9}$, $Gpi^{1.4}$, $Gapd^{0.7}$ and $6Pgd^{0.8}$. The allele $6Pgd^{1.0}$ shows apparently clinal variation: decreasing in frequency from 0.8 in the north to about 0.55 in the southwest, with the south coast samples showing intermediate values. The overall pattern of geographic differentiation on South Caicos thus involves all seven polymorphic loci and is remarkably similar to the pattern revealed morphometrically.

Certain parallels can be drawn between the geographic pattern of genetic differentiation seen on South Caicos and that found previously in the northern Bahamas. On New Providence Island, for example, we found two imperfectly isolated species with an interspecific D of about 0.05 (Gould and Woodruff, 1986). The two taxa showed consistent differences in shell morphology and distribution. *C. glans*, typically with unmottled strongly ribbed shells, is restricted to coastal sites within 3–7 km of the edge of the island bank. *C. gubernatorium*, on the other hand, has mottled finely ribbed shells and is found in the interior of the island and on coasts adjacent to the bank interior. It has not been found at the bank edge. Today the two species hybridize and morphological hybrids have been collected over distances of <1 km where the ranges come into contact. Genetic introgression is, however, more extensive: *C. gubernatorium* alleles have swept into the bank-edge coast populations of *C. glans* and *C. glans* alleles have introgressed 3 km beyond the limits of morphological hybridity. Today, we find genetically "pure" *C. gubernatorium* restricted to the southeast corner of this narrow island (average width 7 km) where they are 5–7 km away from the influence of *C. glans*. The genetic hybrid zone on New Providence is an area of genetic anomaly. Hybrid populations may show

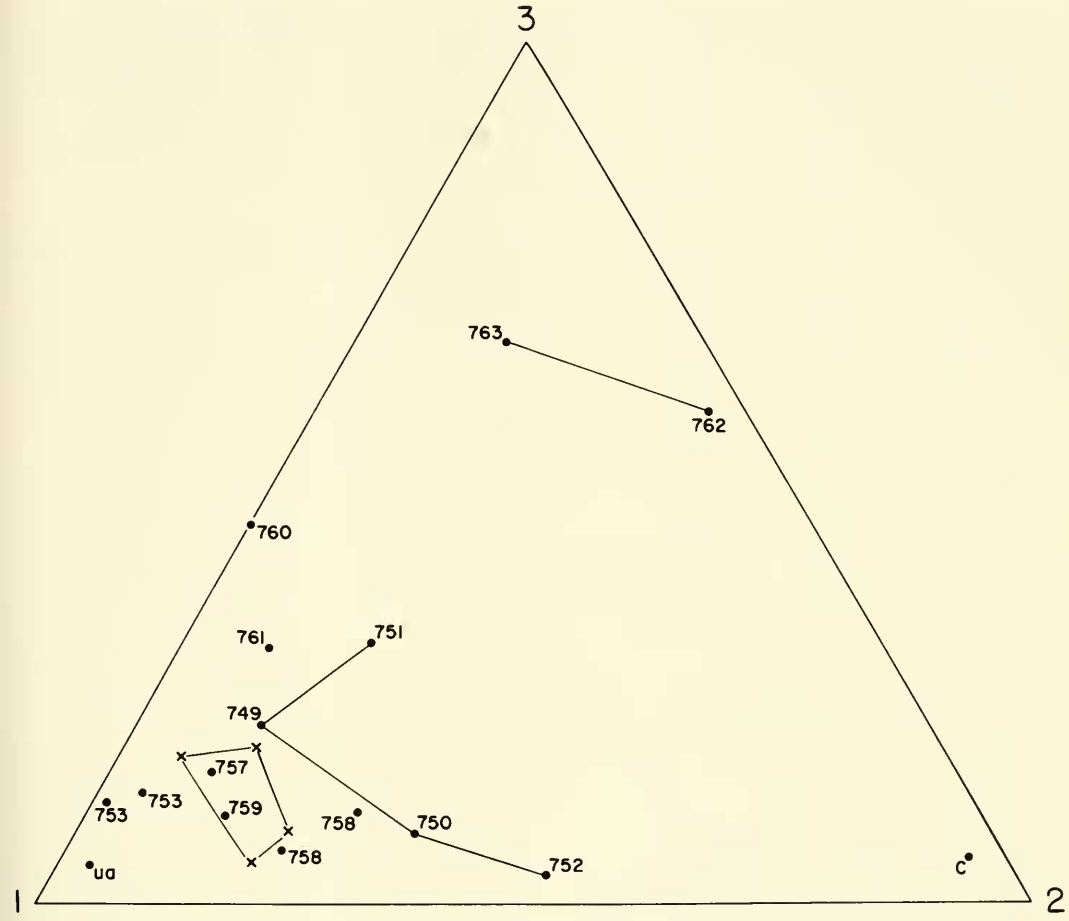

Figure 16. Loadings for South Caicos samples on first three varimax axes. Symbols as on Figure 14.

slightly elevated levels of genetic variability (P, H) and are frequently characterized by the segregation of rare or unique alleles at frequencies far higher than those seen in homospecific populations (Woodruff, 1981). In addition, several step clines in allele frequencies are associated with the hybrid zone. The pattern of clinal variation (bank-edge to bank-interior coasts) of several alleles on New Providence ($6Pgd^{1.0}$, $Es\text{-}2^{1.09}$, $Pgm\text{-}2^{1.2}$) is, in fact, quite similar to that seen on South Caicos and Providenciales. The obvious question arising from the similarities of New Providence and South Caicos is whether today's South Caicos populations represent the legacy of a historical interaction between two species? Has the evidence for a former bank-interior species all but disappeared on this smaller island?

If the Caicos Bank had been originally occupied by a bank-edge and a bank-interior species comparable to those seen on the Great Bahama Bank and the Little Bahama Bank islands, we would make two predictions about the situation on South Caicos based on our earlier work. First, the island is too small for genetically "pure" populations of the interior taxon to endure. All living populations are found within 7 km of the bank-edge and will therefore be introgressed to varying degrees. Present

island size limits our ability to examine this prediction. Nevertheless, additional collecting on bank-interior coasts of North Caicos, Grand Caicos and East Caicos might illuminate this issue as such populations live >10 km from the modern bank-edge coasts. Second, we would predict that the populations furthest from the bank-edge coasts will show more evidence for hybridity than those at the coast. Such interior populations as 764 and 762 might show elevated levels of *P* or *H*, increased heterozygote deficiency or excess, or higher frequencies of rare or unique alleles. There is, however, no evidence for consistent geographic trends in *P*, *H*, or departure from random mating. Only in the case of the rare allele phenomenon are the interior populations at all unusual. Unexpected alleles were, in fact, detected in samples 764 and 762 at Aat^{07}, $Es\text{-}2^{11}$, $Es\text{-}2^{12}$, and $6Pgd^{08}$ at frequencies of 0.02–0.05. Additional rare alleles occurred at 759–761, sites which are also geographically intermediate between the bank-edge and the bank-interior coasts: $Pgm\text{-}2^{13}$, $Mdh\text{-}1^{12}$, Aat^{04}. Two of these rare alleles ($6Pgd^{08}$ and $Es\text{-}2^{11}$) were also detected on Providenciales in sample 772 from the southern bank-interior coast. These rare alleles may be a legacy of a former hybrid zone—that is, they may constitute the genetic anomaly seen in other *Cerion* hybrid zones. Alternatively, these currently rare alleles may once have occurred at higher frequencies in the conspecific bank-interior populations of *C. regina* that until a few thousand years ago occupied an area 20 times as extensive as today's islands.

These hints of genetic vestiges for another taxon within *C. regina* are intriguing (see final section), but do not alter our conclusion that all indigenous *Cerion* so far collected in the Turks and Caicos (excluding the recent immigrants *C. blandi* and *C. lewisi*) belong to the single species *C. regina*. Interspecific hybridization is so rampant in *Cerion* (Woodruff and Gould, 1987) that most widespread species of *Cerion* probably maintain, at least in parts of their range, introgressed genetic material of other taxa. When these introgressed contributions are minor and, especially (as here) when they are associated with no morphological expression of intermediacy, we must retain the name of the dominant component.

We faced the same problem in determining the proper name of the mottled morphotype on New Providence Island (Gould and Woodruff, 1986). *C. gubernatorium*, the oldest name, was originally given to populations that contain "phantom" genes of *C. agassizi*, a prominent fossil taxon now extinct on New Providence, but still living on the adjacent islands of Cat and Eleuthera (and also hybridizing with mottled *Cerion* in both places). Despite these genetic "phantoms," and some morphological remnant of *C. agassizi* as well, we accepted *C. gubernatorium* as the correct name for all mottled *Cerion* of New Providence because the *C. agassizi* signature in these populations is so small relative to the morphological and genetic expression of ordinary (and abundant) mottled *Cerion*. The evidence for phantoms of another taxon within some samples of *C. regina* is far weaker, and shall not alter our taxonomic conclusion that all known Turks and Caicos samples of the tapering morphotype belong to the single species, *C. regina*. We must, however, bear in mind what is no longer only the intriguing possibility, but by now the established fact that important features of geographic variability within many *Cerion* taxa are the product of introgression, not simple local adaptation.

VIII. Level Four: Covariation Within Samples

Variation in average form among samples (treated in all previous sections), and differences among organisms within a population, are so fundamentally distinct in concept that we anticipate no necessary relationship between their patterns. Yet all *Cerion* species grow with the same allometries (despite enormous differences in

TABLE 11. SCORES FOR FIVE-AXIS SOLUTION OF SPECIMENS WITHIN SAMPLE 753.

Measure	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
1. PROWID	0.242	0.020	0.240	0.125	−0.130
2. FOURWID	0.387	0.166	0.075	0.094	−0.025
3. NUMWHO	−0.216	−0.402	0.133	0.027	0.024
4. RIBDENS	−0.064	−0.084	0.358	0.206	0.071
5. LENGTH	0.065	−0.314	0.075	−0.158	0.054
6. WIDTH	0.308	−0.109	−0.009	−0.220	0.180
7. PROHT	−0.117	−0.052	0.539	−0.144	0.204
8. FOURHT	0.205	0.168	0.408	0.106	−0.116
9. FRSXHT	0.365	0.178	0.179	0.113	−0.051
10. UMBWID	0.013	0.126	0.320	0.184	0.367
11. LIPWID	0.258	−0.089	−0.061	0.101	0.143
12. LIPTHK	0.019	−0.239	0.029	0.185	−0.045
13. APHT	0.287	−0.094	−0.085	−0.233	0.443
14. APWID	0.254	−0.147	−0.181	−0.033	0.317
15. APROT	−0.065	−0.041	−0.058	0.476	0.294
16. EC	0.075	−0.407	−0.088	0.245	−0.245
17. FA	0.259	−0.295	0.194	−0.205	−0.352
18. APTILT	−0.131	−0.024	−0.030	0.435	0.191
19. WEIGHT	0.049	−0.292	0.092	−0.129	0.175
20. HWRATIO	−0.140	−0.344	0.190	0.063	−0.079
21. PRORAT	0.304	−0.042	−0.119	0.342	−0.264
22. FOURRAT	0.175	−0.243	−0.203	0.158	0.130

outcome), and the gastropod shell, in general, is a highly constrained structure replete with geometrically forced covariances. Thus, we expect that similar patterns might regulate the different styles of within- and among-sample variation (see Gould and Paull, 1977; Gould and Woodruff, 1978 for correspondences in other *Cerion* species). Sample means might represent different states along tracks of covariance common to the within-sample variation of all populations.

Since all shells are adults and their range in size is not large, our samples of 20 do not provide enough specimens for stable covariance structures within populations (though they define mean values adequately). But we measured a larger number of shells (as a split sample to test for proximity in morphospace) for South Caicos *C. regina* at locality 753 (35 individuals). Table 11 presents factor scores for this enlarged sample. The structure of covariation is stable at five meaningful axes (93.2% of information). (In a sequence of reduction from 10 axes down, none of the first five axes ever dip below 7%, and no subsequent axis reaches 2% of total information.)

The first axis unites the two major patterns of constrained covariance that we have discussed throughout this paper. First, we see all chief components of the compensatory (flat top with later height) covariance that sets the primary pathway of variation in shape from obtusely triangular in cross section throughout, to distinctly flat topped at first, and parallel-sided during later growth. Note high scores for the two ratio measures of flat top (width/height of protoconch at 0.304, and of the fourth whorl at 0.175). Protoconch width (0.242) greatly exceeds protoconch height (negative at −0.117), but height is beginning to catch up by the fourth whorl (0.387 for width, 0.205 for height). The three scores for successive heights increase continually to record the compensation (−0.117 to 0.205 to 0.365).

Second, we note all elements of the major constraint imposed by geometric necessity: large whorls imply fewer adult

whorls under conditions of restricted range in adult size. Intermediate standardized whorl sizes score highly (fourth width and height at 0.387 and 0.205, and fourth to sixth height at 0.365). These large whorls imply fewer total whorls (−0.216), with the usual consequence of squatter adult shells, since later whorls add relatively more height than width (height/width ratio of adult shell at −0.140).

The second axis primarily records whorl number (−0.402) and its consequences in shape for a high, but not wide, shell (−0.314 for height, −0.109 for width, since later whorls add relatively more height than width), and final shape (height/width ratio at −0.344). This primary association also brings along, as on axis 1, the forced negative covariances with standardized whorl sizes (0.166 for fourth width, 0.168 for fourth height, 0.178 for fourth to sixth height).

The highest scores on the third axis are for early standardized heights (0.539 for the protoconch, 0.408 for the fourth whorl), with protoconch width also scoring at 0.240. We do not understand the basis for associated high scores of umbilicus (0.320) and density of ribbing (0.358).

The smaller fourth and fifth axes express different aspects of the third allometric phase that builds *Cerion*'s aperture. The fourth axis records its two highest scores for measures of intensity in the change of orientation made by the growing edge before it deposits the definitive adult aperture (0.476 for apertural rotation, 0.435 for tilt). The fifth axis records the size of the expanded apertural mouth (0.443 and 0.317 for apertural height and width, associated with negative values for the penultimate whorl heights overgrown by this expansion, −0.245 and −0.352 for measures 16 and 17).

In summary, each axis makes sense in terms of both the general geometry of shell coiling (the whorl size versus whorl number principle for example), and the peculiarities of *Cerion*'s own universal pattern of growth (the apertural changes at adulthood, and the allometric compensation of flat top by later height, for example). We find interesting similarities and differences with patterns of covariation at the between-sample levels considered earlier. Dominating the within-sample system, we find two covariance sets that also regulate variation among mean vectors of *C. regina* samples—the compensatory shape covariance (setting axis one here), and the negative interaction of whorl size and number (expressed on both first and second axes). Most different from between-sample patterns are the greater strength of these two covariance sets, and absence of the general size factor that played an important role at all higher levels. Interestingly, these two differences are causally related. The size factor is absent here for the simple reason that size varies little among adults within most populations (length ranges from 27.0 to 34.0 mm in this sample), but greatly in mean values among populations (see appendix). The constraint covariance (whorl size versus whorl number) only operates when size ranges are small and restricted (see Gould and Paull, 1977 for quantitative demonstration)—for if adult size is free to vary, then large early whorls need not be compensated by growing fewer whorls to reach a limited final size.

To assess the generality of these within-sample covariances across taxa, we present, as Table 12, factor scores for the four large and interpretable axes (90.9% of information) of a *C. lewisi* sample (No. 221564, see appendix). The axes are remarkably similar to those noted just above in *C. regina*. High scores on the first axis emphasize *C. lewisi*'s chief character of many whorls and its consequence for slender shape (0.484 for whorl number, 0.323 for adult height, with adult width much less at 0.170, and 0.281 for height/width ratio of the adult shell). But we also note the constraint covariance, operating on this axis in the negative scores for standardized whorl sizes (−0.104 and −0.099 for protoconch and fourth width; −0.203 and

TABLE 12. SCORES FOR FOUR-AXIS SOLUTION OF SPECIMENS WITHIN A SAMPLE OF *C. LEWISI*.

	Measure	Axis 1	Axis 2	Axis 3	Axis 4
1.	PROWID	−0.104	0.362	−0.241	0.032
2.	FOURWID	−0.099	0.130	−0.185	0.171
3.	NUMWHO	0.484	−0.095	0.003	−0.024
4.	RIBDENS	0.344	0.284	0.434	0.133
5.	LENGTH	0.323	−0.050	−0.072	0.209
6.	WIDTH	0.170	−0.035	−0.209	0.140
7.	PROHT	0.048	0.330	0.210	0.140
8.	FOURHT	−0.203	0.454	−0.013	0.279
9.	FRSXHT	−0.178	0.315	−0.188	0.098
10.	UMBWID	0.036	0.309	0.143	0.014
11.	LIPWID	0.147	0.196	−0.324	−0.155
12.	LIPTHK	0.193	0.167	−0.042	−0.181
13.	APHT	0.123	−0.099	−0.240	0.306
14.	APWID	0.080	−0.155	−0.290	0.166
15.	APROT	−0.050	−0.109	−0.100	0.468
16.	EC	0.125	0.010	0.004	0.359
17.	FA	0.258	0.327	−0.119	−0.182
18.	APTILT	0.054	−0.092	0.023	0.430
19.	WEIGHT	0.208	0.036	−0.094	0.008
20.	HWRATIO	0.281	0.081	0.139	0.063
21.	PRORAT	−0.054	0.114	−0.437	−0.100
22.	FOURRAT	0.352	−0.011	−0.278	−0.153

−0.178 for fourth, and fourth to sixth whorl height).

The second axis, as did the third in *C. regina*, emphasizes standardized whorl sizes and little else. We are again puzzled that both ribbing (at 0.284) and umbilical width (at 0.309) also score strongly, for they did in *C. regina* as well, and we do not understand the basis for such an association—though its discovery in two taxa suggests a possible generality.

The third axis expresses the compensatory shape covariance that so dominates geographic sorting (both within and between islands) of *C. regina*, and also the first axis of within-sample covariation in *C. regina* sample 753. Its existence in *C. lewisi* supports our claim that this association is an important principle governing *Cerion*'s shape throughout the genus. The shell begins flat, with high score for protoconch width (−0.241) and opposite score for protoconch height (0.210—the factor loadings of all specimens are negative on this axis, so we discuss negative scores as high values). This initial flatness is recorded in high scores for width/height ratios of protoconch (−0.437) and fourth whorl (−0.278). But later heights compensate, and we note the continual gradient in scores for the three standardized heights that we have observed so many times before (+0.210, −0.013 and −0.188 for protoconch, fourth, and fourth to sixth whorls).

The fourth axis amalgamates the two apertural covariance sets that formed the fourth and fifth axes of *C. regina*. We note high scores for the two measures of change in orientation (0.468 for rotation, 0.430 for tilt) and for apertural size (0.306 for height, 0.166 for width).

The patterns of within-sample covariance for representative samples of two species are therefore similar to each other, and different from between-sample patterns in the same ways. In both, we find no general size axis since the within-sample range of shell size is small. In both, the compensatory shape covariance (flat top and later height) and the constraint covariance (whorl size versus whorl number) dominate the larger axes. The constraint

covariance appears more strongly in these within-sample patterns because it only operates when the range of final size is limited. In both samples, we also find sensible associations for measures of the aperture and standardized whorl sizes. We believe that we are here looking through a glass not so darkly at the general rules of growth within *Cerion*.

IX. Conclusion and Prospect

This work begins the second half of our long-term project to revise the Bahamian *Cerion* in the light of new data and contemporary concepts of evolution. It is our initial study, following our strategy of beginning with geographic outliers that maintain low diversity, of *Cerion* faunas in the southeastern Bahamas—a group of species different from those of Great and Little Bahama banks, the subjects of our previous work. We will move from here to the complexity of the largest island, Great Inagua, where more taxa (about 20) have been designated, and at least three widespread indigenous species actually exist.

A close relative of *C. regina* inhabits the long bank-edge northern coast of Great Inagua. But Inagua is big and diverse enough to maintain other indigenous *Cerion* species—including the vast populations of the island interior and bank-interior coasts (now called *C. rubicundum* and *C. dalli*, but probably belonging to a single species), and the widespread dwarfed *C.* (*Umbonis*) that lives in true sympatry (the first unambiguously recorded case in the entire genus *Cerion*) with both bank-edge and interior species. The small islands that we studied in the Turks and Caicos maintain only the bank-edge species as a widespread, indigenous form—but they permit us, by extension, to grasp the greater complexity of Inagua.

It is often said of historical sciences like ours (said, that is, by those who would degrade our activity, or bar us completely from the realm of science) that we traffic only in the narrative description of particulars and that we never predict or derive any generalities worthy of the name. Narrative must be treasured in its own right (for it can be every bit as factual as anything in science), but science must aspire to more—as historical science does, despite the caricatured dismissal outlined above.

The complexities and contingencies of history do preclude detailed prediction of future events, but prediction of this sort does not lie within our domain. Yet historical scientists work with a sort of prediction all the time—of events that have happened but have not yet been revealed by evidence, or of current situations inferred but not yet validated. In this essential component of generalization, natural historians work like all scientists.

Yet many of our subjects are so resolutely particular that we cannot proceed beyond simple narrative; thus, we must seek and exploit those situations of sufficient repetition to permit the apprehension of general pattern within the particulars. The attraction of *Cerion* lies in its central source of both narrative and generality—its overwhelming diversity, repeated in all ways that we can study: morphologically, genetically, biogeographically, ecologically.

Thus, we feel that we can creep to the end of an inferential limb and predict (based on genetic hints) that a second indigenous, geographically interior taxon may still persist (either as relatively pure populations or as substantial introgressed contributions to *C. regina*) in the centers of large islands on the Caicos Bank. We say this for two reasons: first, we have traced central distinctions between bank-edge and interior taxa on many other islands; second, we can often document the disappearance of the interior taxon on small islands that are, so to speak, "all" bank-edge, while the interior taxon persists on adjacent larger islands (for example, both bank-edge and interior *Cerion* live on Great Exuma, but only the bank-edge species on all the small adjacent cays). We also predict (based on repeated pattern from nearby Great Inagua), that should

this interior taxon be found, it will bear a smaller, thinner and more mottled shell than typical *C. regina* (we base this inference on the bank-edge versus interior distinction on all other islands, and particularly on the Inaguan separation between interior *C. rubicundum* and *C. columna*, the bank-edge analog of *C. regina*).

Likewise, our studies of allometry and ontogenetic covariance provide a basis for ordering variation within species (and often between hybridizing taxa) in a sensible way. The patterns dictated by what we have called the constraint and compensatory covariances are sensibly interpreted as necessary outcomes of *Cerion*'s basic ontogeny; they then determine the correlated consequences of any primary change in size or shape. And they occur over and over again in predictable manners and circumstances.

We find it intellectually satisfying that the primary component of narrative—*Cerion*'s buzzing and blooming outpouring of diversity—also becomes raw material for the repetitions that science requires for discussing general pattern. As great naturalists (G. E. Hutchinson, for example) exemplify by their life and work, exultation and explanation are complementary aspects of nature and its impact upon our minds.

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